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The following errors were noted after printing.

Page 17: The caption for Figure 2 should read: Fig. 2. In shallow waters *Ruppia maritima* shows a more compact growth form with pronounced forking of stems and short internodes.

Page 18: The caption for Figure 3 should read: Fig. 3. Elongate life form of *Ruppia maritima* as a result of growth in deeper waters. Longer internodes between branches are typical.

We sincerely apologize for any inconvenience this may cause you.



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Wigeongrass (*Ruppia maritima* L.): A Literature Review

By Harold A. Kantrud

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

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Wigeongrass (*Ruppia maritima* L.): A Literature Review

by

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Abstract. Wigeongrass (*Ruppia maritima* L.) is a submersed macrophyte of nearly cosmopolitan distribution and worldwide importance as a waterfowl food. Unfortunately, the plant no longer inhabits vast areas disturbed by human activities. Taxonomic status of the plant is uncertain, especially in North America. In mild climates, in habitats subject to environmental extremes, the plant behaves as an annual (vegetation perishes), or as a perennial in deeper, more stable habitats (some vegetative parts grow year round). Drupelets (seeds) provide a mechanism for wigeongrass to survive periods of drought and excessive water salinity. These sexual propagules can be washed ashore or carried by birds or fish for long distances.

Wigeongrass mostly occurs in temporarily to permanently flooded mesohaline–hyperhaline estuarine wetlands, but it also occurs inland in fresh to hypersaline palustrine and lacustrine wetlands. Most populations inhabit warm, relatively unpolluted, and well lit waters <2.0 m deep where fetches and wave action are not great. The species is probably best adapted to stable water levels but can tolerate significant water level fluctuations, including periodic exposure in tidal areas. Robust growth occurs in areas of slow current. Wigeongrass is alone among the submersed North American angiosperms in tolerance to high salinity, but it is likely at a competitive disadvantage among specialist taxa in soft or acidic waters. The species grows in nearly all common bottom substrates, but growth is favored by aerobic and low H₂S conditions. Turbidity frequently limits wigeongrass growth in waters overlying easily suspendible bottom substrates.

Wigeongrass often occurs in monotypic stands, yet grows with many other submersed and emergent macrophytes. Dominance in certain wetlands sometimes alternates with dominance by other submersed macrophytes as salinities, seasonal temperature cycles, or other environmental factors change. The shading effect of metaphytic, planktonic, or epiphytic algae often reduces production.

Wigeongrass and its detritus provide food and cover for a large invertebrate biota, although direct consumption of the living plants is minimal. Wigeongrass beds in coastal wetlands are heavily used by fish. The plant is recognized worldwide as an important food of migrant and wintering waterfowl, wading birds, and shorebirds. In subtropical climates, wintering waterfowl can quickly consume entire stands.

Propagation and management of wigeongrass has occurred for nearly 60 years in the southern and eastern United States. During the seventies and eighties, sophisticated water level and salinity management techniques have been developed to encourage growth of the plant.

Future research should concentrate on determining the means to reduce light-limiting turbidity in many wetland types; understanding the ways in which human activities on and near wetlands affect wigeongrass production; and developing reliable and predictable techniques to stimulate wigeongrass production by water level manipulations and other means in different environmental settings. Trophic interactions and the effects of biomanipulation of fish populations in managed wigeongrass habitat—now little understood—also require more study.

Key words: Wigeongrass, *Ruppia maritima*, autecology, physiology, production, habitat, economics, management.

Throughout the world, communities of submersed angiosperms attract waterfowl, fish, and many other organisms to feed and rear their young. Wigeongrass (*Ruppia maritima*) dominates some of the communities most important to waterfowl. To properly protect and manage these resources, understanding the ecology of these communities is essential.

Early in this century, McAtee (1915) noted that "bays that have kept their wigeon-grass have kept their ducks; those in which the plant has been destroyed by influxes of mud and filling up of the inlets have lost them." The plant remains abundant in some areas (Chabreck 1972) but nevertheless has continued to decline in many wetlands that have a history of substantial use by waterfowl (Saunders and Saunders 1981). Thus, efforts are under way in several countries to restore wigeongrass and other important waterfowl food plants to their former abundance. The success of these endeavors requires applying a thorough knowledge of the life histories and environmental requirements of these taxa.

There are two brief life histories of wigeongrass (Stevenson and Confer 1978; Wallentinus 1979) and several dozen important papers on the effects of various environmental variables on the plant. The most comprehensive work on wigeongrass is a series describing the autecology, synecology, production, consumption, and decomposition of *Ruppia*-dominated communities in western Europe (Verhoeven 1979, 1980a, 1980b). Wigeongrass receives little use as a test plant for laboratory culture and has few properties that are objectionable to humans. Thus, little information is available on the physiology and control of wigeongrass. However, because wigeongrass is important to waterfowl, considerable information is available on methods to establish and manage the plant. Much of this information comes from studies in the southern and southeastern United States.

This report outlines the life history and management of *R. maritima*, probably the most important of all *Ruppia* taxa for wildlife, at least in the Northern Hemisphere. Information in this report comes mostly from papers written in English or with English summaries.

Classification and Distribution

The valid scientific name for wigeongrass is *Ruppia maritima* L. as assigned by Linnaeus in his *Species Plantarum* of 1753. He described the genus in *Genera Plantarum* (Linnaeus 1737), referring to a plate in Micheli's (1729) *Nova Plantarum Genera* (Setchell 1946). The generic name is dedicated to the German botanist Heinrich Bernhard Ruppius (1689–1719) and the specific epithet *maritima* means "of the sea" in botanical Latin (Fernald 1950). Since Linnaeus's time there has been much disagreement among taxonomists whether more than the type species (*R. maritima* L.) should be recognized in the Northern Hemisphere, or whether clinal variations in morphology and reproductive behavior are expressions of adaptations of the species to a diversity of habitats (Phillips 1958; Richardson 1980).

Hutchinson (1959) placed the genus *Ruppia* in the family Ruppiaceae. Kartesz and Kartesz (1980) place the genus in the family Zosteraceae. They recognize three North American (including Greenland) species of *Ruppia* (*R. anomala*, *R. cirrhosa*, and *R. maritima*) and list nine varieties of *R. maritima*. Older North American floras, phytogeographical studies, and waterfowl food-habit studies often differentiated *R. occidentalis* ("western wigeongrass") from *R. maritima*. Many taxonomists now consider the plant a variety of *R. maritima*. Morphological variations of the plant caused by the environment may impose taxonomic problems in interior North America (Hammer and Heseltine 1988). In Europe, the genus is considered a member of the family Potamogetonaceae, and two species (*R. cirrhosa* and *R. maritima*) are recognized (Verhoeven 1975, 1979). These species are separated by morphology and chromosome number (Reese 1962) and the salinity, depth, and water permanence of the wetlands they inhabit (Verhoeven 1975; Verhoeven and Van Vierssen 1978b). Australia has four species (*R. maritima*, *R. megacarpa*, *R. polycarpa*, and *R. tuberosa*) that are also placed in the Potamogetonaceae (Bayly and Williams 1973; Brock 1982a; Jacobs and Brock 1982). Other species, varieties, and

forms of this taxonomically and nomenclaturally confused genus are recognized from similar habitats in other parts of the world (Verhoeven 1979). Van Vierssen et al. (1981) urges taxonomic study of the genus on a global scale.

Wigeongrass (McAtee 1935) is sometimes spelled "widgeongrass" or "widgeon-grass," but I have maintained the cited common name because of the officially accepted (American Ornithologists' Union 1983) common names, American and Eurasian wigeon (*Anas americana* and *A. penelope*). Other common or colloquial names for wigeongrass include "ditch-grass," "duck grass," "fines," "niggerwool," "peter-grass," "puldoo-grass," "sea grass," "swan grass," "tassel grass," "tassel weed," "tassel pondweed," and "zhebes" (McAtee 1915, 1939; Setchell 1924; Ferguson-Wood 1959).

Most of the information on wigeongrass in this report applies to the genus, or *Ruppia maritima* s.l. (i.e., *sensu lato*, meaning the species in its widest sense), except where references show that differences in morphology, growth form, habitat, or other features exist among the six aforementioned species. In these cases, I follow the lead of Verhoeven (1979) and present data only for *Ruppia maritima* s.s. (i.e., *sensu stricto*, meaning the species in its narrowest sense). *Ruppia maritima* s.s. from northern Europe normally has $2n = 20$ chromosomes, but some southern populations have $2n = 40$ (Van Vierssen et al. 1981; Aedo and Fernandez Casado 1988).

Fossil *Ruppia* pollen from the North American Pleistocene (Martin 1963) and *R. maritima* drupelets from the Holocene (Pierce and Tiffney 1986) are known.

Autecological Classification

Although often found with the seagrasses, wigeongrass (Fig. 1) is not a true marine plant but considered a freshwater species with a pronounced salinity tolerance (Zieman 1982). Verhoeven (1979) considers *Ruppia* to have little competitive strength outside its rather well defined ecological niche, and he states that its survival is inhibited by competition in certain freshwater and marine habitats that would otherwise be physically suitable. Even in suitable habitats, frequency and biomass of wigeongrass varies greatly, both temporally and areally (Davis et al. 1985).

Ruppia maritima s.l. behaves as an annual (vegetation perishes) in habitats subject to drought, lethal increases in salinity, or other extremes; or as a pe-

rennial (at least some vegetative parts grow year round) in deeper, more stable environments (Richardson 1980; Bigley and Harrison 1986). For wigeongrass behaving as an annual, Bigley and Harrison (1986) describe its demography as "rapid production and early death of ramets (individual plants of clones) after production of seeds." Richardson (1980) noted that, early in the growing season, plants with annual growth habit likely have an affinity for areas of low salinity attributable to their requirement of rapid germination and fruit production before salinity maxima, occur. In more saline waters, he found forms with perennial growth habit.

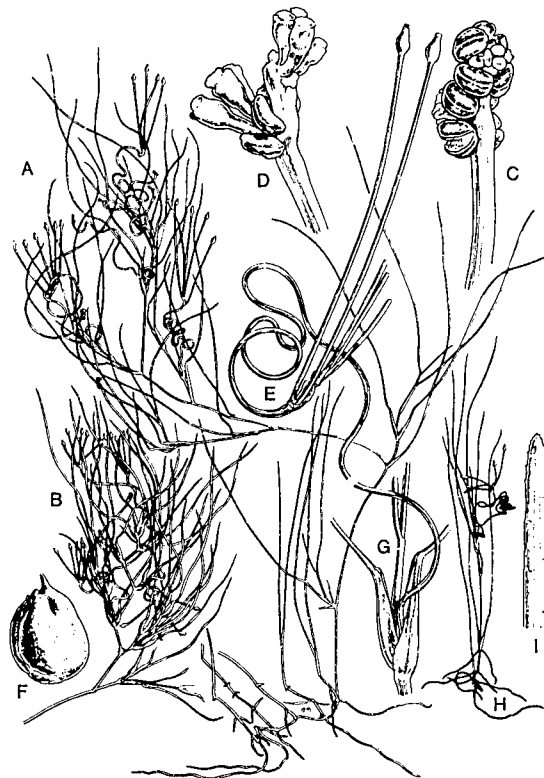


Fig. 1. *Ruppia maritima*: A and B, variations in habit, the stems sometimes very long and slender or sometimes with short zigzag nodes, $\times 0.5$; C, spike consisting of peduncle and inflorescence bearing two young flowers, each consisting of two large, bicellular anthers and four pistils, $\times 10$; D, two flowers, after fertilization, $\times 10$; E, development of the long-pedicelled fruits following fertilization of the two flowers (note elongated, coiled peduncle), $\times 2.5$; F, mature drupelet, hard and black, $\times 10$; G, two stipular sheaths of the alternate, capillary, succulent leaves, $\times 2.5$; H, habit variation, $\times 0.5$; I, serrate leaf tip, $\times 25$ [from Mason (1969) with permission from the University of California Press].

Plants in some wetlands alternate between perennial and annual life cycles (Koch and Seeliger 1988). Setchell (1924) believed perennial forms grew mostly in areas subject to tidal conditions that left plants exposed or covered with shallow to deep water, whereas annual forms grew in shallow ponds with less tidal influence. In culture, however, plants thought to be annuals flourished throughout the year and produced abundant fruit.

Plants from more stable environments generally are taller, have wider leaves, and produce fewer sexual propagules (Verhoeven 1979). These plants also have longer flower peduncles—so pollination occurs at, rather than under, the water surface—and larger, stronger root systems that allow vegetative hibernation.

The growth form of wigeongrass, as seen in culture experiments, is also dependent on sediment chemistry. Plants supplied with low levels of inorganic nutrients in a washed-sand substrate grew many short shoots from an extensive network of rhizomes and roots, whereas those supplied with organic nutrients grew as long vertical shoots from reduced belowground parts (Pulich 1989).

In shallow sites, wigeongrass concentrates much leaf area just above the bottom (Wetzel et al. 1981). In deeper waters, plants often grow in a form termed by Hutchinson (1975) as parvopotamid—that is, a higher aquatic plant, rooted in sediment, perennially submersed except inflorescences, and having long stems and small, mostly undivided leaves. Luxuriant parvopotamid growth results in dense leaves, branches, and inflorescences in the upper part of the water column, but much thinner density of stems and widely-spaced leaves below. Vegetative density of the upper part increases with falling water levels (Verhoeven 1980a). Verhoeven (1980a) recognized three horizontal growth patterns in *Ruppia*-dominated communities in Europe: dense monospecific beds, mosaics of sharply delimited patches, and beds of mixed species that formed patches often touching or penetrating each other. He also found several examples of horizontal zonation, where plants tended to order along gradients of depth, substrate, or exposure. The most common pattern was where short-lived forms of wigeongrass occupied nearshore areas (with temporarily or intermittently exposed water regimes) and perennial forms inhabited deeper offshore areas in a mosaic pattern with sago pondweed (*Potamogeton pectinatus*). Many other growth forms for aquatic macrophytes have been described (Hutchinson 1975). Communities supporting wi-

geongrass are noted for a poverty of such forms; most European stands assume the parvopotamid form but are sometimes mixed with filamentous algal, charid, and zosterid forms (Verhoeven 1980a).

Classifications of *Ruppia*-dominated stands by the Braun-Blanquet (1931) phytosociological system popular in Europe (e.g., Gillner 1960; Westhoff and Van der Maarel 1973; Beeftink 1977) will not be outlined here.

Distribution

Worldwide distributional records for *Ruppia* taxa show that representatives of the genus occur on all continents of the world and on many islands. The northern limit is about 69°N, the southern limit is at least 55°S, and the altitudinal limit is at least 3,800 m above sea level (Verhoeven 1979).

Development and Reproduction

Except where specific references are given, information in this section on *R. maritima* s.l. and comparisons with other *Ruppia* taxa were excerpted from the sources listed in Table 1 and standard botanical texts.

Roots and Rhizomes

Nearly 100% of the belowground biomass (roots, rhizomes, and root hairs) of wigeongrass usually lies in the upper 10 cm of the bottom substrate, and sometimes nearly 90% is in the upper 5 cm. In temperate estuaries, where the plant behaves as a perennial, the dry weight of belowground parts during peak growth can vary from 76% of total plant dry weight in extremely shallow sites to only 2% in deeper sites. This may reflect different strategies for nutrient uptake or survival in dimly lit waters. Belowground biomass averages about 30–45% of maximum seasonal biomass. The belowground biomass develops best at well oxygenated sites in coarse-textured bottom sediments. Complete degeneration of the system can occur in very highly reduced organic bottoms.

A single wigeongrass plant can have 2–15 rooting nodes on the rhizome. Short-lived roots up to 20 cm long occur singly or in groups of up to 20 at the nodes. Roots can compose 16% of the dry weight of

Table 1. *References and subject material on development and reproduction of Ruppia.*

Reference	Subjects discussed	Reference	Subjects discussed
Graves 1908	Morphology, functional anatomy, and environmental adaptations of organs	Verhoeven 1979	Taxonomy, dispersal mechanisms, pollination, fructification, and drupelet germination
Fernald and Wiegand 1914	Taxonomic descriptions of North American <i>Ruppia</i> varieties	Richardson 1980	Growth habits in relation to environmental factors
Fernald 1950	Morphology	Wetzel et al. 1981	Community structure and biomass allocations
Jemison and Chabreck 1962	Drupelet production	Harrison 1982	Anatomy, plant weights, and drupelet germination
Conover 1964a	Functional anatomy of roots	Jacobs and Brock 1982	Taxonomy and descriptive characters
Gore 1965	Drupelet germination	Orth and Moore 1982	Biomass allocation, shoot densities, and growth rates
Conover and Gough 1966	Morphology and functional anatomy of belowground parts	Bigley and Harrison 1983, 1986	Shoot demography and morphology
Joanen and Glasgow 1965	Drupelet germination	Brock 1983	Growth forms and reproductive allocation in annual and perennial <i>Ruppia</i> taxa
Mason 1967	Morphology and functional anatomy	Kadlec and Smith 1984	Drupelet germination
McMillan and Moseley 1967	Asexual reproduction	Seeliger et al. 1984	Drupelet germination
Ortu 1969	Drupelet germination	Thursby 1984a, 1984b	Drupelet germination and root hair measurements
Weldon et al. 1969	Morphology	Thursby and Harlin 1984	Nutrient uptake by leaves and roots
Mayer and Low 1970	Plant weights, drupelet germination	Van Vierssen et al. 1984	Drupelet germination: effects of salinity, temperature, and other environmental factors on
Thiret 1971	Asexual reproduction	Pulich 1985, 1989	Seasonal growth dynamics and nutrient uptake
Davis and Tomlinson 1974	Comparative anatomy and morphology	Koch and Seeliger 1988	Drupelet germination
Posluszny and Sattler 1974	Floral development		
Richardson 1976	Pollination mechanisms		

cultured plants 3 weeks old. A zone of dense (up to 60/mm²), relatively short (<1 cm) root hairs occurs toward the distal end of each root. Although sheaths (coleorrhiza) partially protect wigeongrass roots from desiccation and physical damage, the root system is delicate and unable to penetrate deeply into sediments. This makes the species susceptible to water turbulence.

Wigeongrass cultures easily without sediment, but roots probably serve some function because detached plant parts and the top ends of vertical stems >1 m long will quickly form roots. Experiments show that

roots do not act independently of leaves in nutrient uptake. Roots of wigeongrass growing in highly reducing sediments probably receive oxygen through the plant's lacunar system.

The main underground body of wigeongrass is a rhizome (rootstalk) that branches from a single axis (youngest branches at the tip) with shoots originating at about 1-cm intervals. Rhizomes are anatomically similar to vertical stems except for the presence of roots instead of leaves. Rhizomes contain more starch than upright stems, are thin and pale, and usually lie only a few millimeters below the bottom

surface. The vascular system in rhizomes and roots is extremely simple.

Vegetation

A wigeongrass plant can have 10–15 vegetative shoots per tenth of a square meter during the horizontal branching phase and >20 reproductive shoots per tenth of a square meter during the flowering phase. Over 30,000 shoots per square meter sometimes occur. Shoots produced early in the growing season probably live longer than those produced later, and transition from the vegetative state to the reproductive state increases shoot lifespan. Few shoots that have normal lifespans remain vegetative. Near the end of the growing season, older rhizomes degenerate, leaving ramets that die before winter. Plants subject to exposure to air in intertidal habitats have fewer shoots, a greater number of shoots flowering early in the growing season, and lower drupelet production than plants that remain submerged during the growing season.

Before and during flowering, the thin wigeongrass stems usually grow rapidly, producing numerous lateral branches that branch again, and so on, but nearly stemless plants can also occur. Stems are about 1 mm wide and up to 3 m long, but average plant height is probably about 5–20 cm in most temperate waters. Plants have little strengthening tissue and the surrounding water provides support for dense upper vegetation.

Leaves are alternate, <1 mm wide, <20 cm long, and held by membranous sheaths <7 cm long with short, free tips. Leaf tips vary from obtuse and serrate (Fig. 1) to acute and entire. The proportion of leaf area at various depths reflects adjustments to differences in light regimes caused by turbidity or the presence of other plants. The structure of leaf epidermal cells and their chemical composition varies with water salinity (Jagels and Barnabas 1989).

Flowers

Wigeongrass produces huge numbers of underwater flowers about 5–6 weeks after the onset of spring growth. Two tiny (3–5-mm diameter) bisexual flowers, lacking perianth, are atop one another on a slender fleshy spike. Flowers begin development sheathed inside a pair of subfloral leaves. Each flower has two stamens and four (3–5) pistils. After 1–2

weeks, the spike is pushed out of the swollen sheath by a peduncle that grows rapidly in length. Anthers burst and release pollen, aided by gas bubbles that accumulate inside the anther sac. Some pollen is trapped within the inflorescence and some clings to the surface of the gas bubbles. Most of the eight pistils usually found in each inflorescence are thus self-pollinated, but cross-pollination occurs from the pollen-laden bubbles that rise to the water surface, transporting pollen to other wigeongrass flowers.

Peduncle form is one of the main characters taxonomists have used to split *R. maritima* s.l. into separate species. Annual forms have peduncles that are either short, stiff, and straight or loosely coiled, up to 3 dm long, and that are pollinated underwater. Perennials have flexuous coiled peduncles up to 10 dm long and are pollinated at the water surface. These coiled structures can pull the fertilized inflorescences back underwater.

Sexual Reproduction

Annual *Ruppia* taxa depend on high fecundity to increase chances of reproduction in ephemeral habitats. Important features of this reproductive pattern are rapid development, early maturity, and the allocation of much energy into many small propagules. These taxa have 100% of their biomass in reproductive material (propagules) when wetlands are dry and about 20–30% when plant weights are highest during years of good growing conditions. The propagules of annual *Ruppia* taxa are technically termed drupelets, but are often called “nutlets” or “seeds.” Drupelets can remain viable in sediments for up to 3 years.

Ruppia maritima s.s. produces enormous numbers of drupelets about 2 weeks after first flowering because the many inflorescences are efficiently self-pollinated. The dark brown or black drupelets are 0.5–4 mm long, and vary from obliquely ovoid or rounded to asymmetrical, flattened, and beaked. Salinity may control drupelet size and shape, and drupelets produced in early summer can have a thicker coat than those from the same plant in early fall. Drupelets are attached to slender pedicels that vary in form depending on water conditions. Populations in shallower, more saline waters typically have nearly straight pedicels up to 4 cm long; populations in deeper, fresher water generally have curved, longer pedicels. Pedicels are always longer than the

drupelets. Healthy drupelets average 1–7 mg dry weight (Gore 1965; Prevost et al. 1978). An elliptic or triangular perforation occurs near the base of the beak. A fully pollinated and mature inflorescence usually consists of eight pedicellate drupelets atop a straight or coiled peduncle. A *Ruppia* taxon with up to 12 sessile drupelets occurs in hypersaline Australian wetlands (Brock 1982a).

Ripe drupelets are transported short distances in floating vegetation, considerable distances by wind and in the guts of fishes, and long distances in the digestive tracts of waterfowl. Wigeongrass drupelets mix with small amounts of other plant material, forming compact balls up to the size of small watermelons—these are often found along the beaches of saline lakes in windy locations. Such balls presumably form by wave action (field notes of F. P. Metcalf in McAtee 1925; Essig 1948; Swanson and Springer 1972; Gerbeaux and Ward 1986).

Water permanency, water depth, depth distribution of drupelets in sediment, sediment chemistry, and water column chemistry can influence drupelet distribution and germination and interact with temperature effects. In temperate climates, drupelets usually lie dormant underwater or on desiccated bottoms until the following spring. Most drupelets are found in the upper 5 cm of bottom sediment, but they can occur as deep as 25 cm. Drupelets buried >10 cm in sediment probably do not germinate under natural conditions. Drupelets do not germinate on moist soil but will germinate under as little as 4 cm of water indoors and 5–10 cm outdoors. However, little or no drupelet production occurs from plants germinated and grown at these shallow depths. Germination of *R. maritima* s.l. drupelets in Europe begins when water temperatures exceed the minima-maxima interval of 10–15° C for about 10 days; previous desiccation may stimulate germination. For European *R. maritima* s.s., stratification for 2 months at 4° C increases germination. Temperature at germination usually is about 15–30° C. Drupelets germinate in as few as 8 or as many as 30 days. Drupelets from habitats subject to prolonged drought probably take longer to germinate than those from more permanent water bodies.

Germination of wigeongrass drupelets is greatly reduced where upper layers of sediments contain >1–2% soluble salts or where NaCl (sodium chloride) concentrations in the water exceed 15 g/L. However, drupelets that will not germinate because of higher salinities can recover and germinate after about 2 weeks in fresh water. Germination rate of

drupelets kept in fresher (<3.5 g/L) waters at higher temperatures is lower than for those kept at lower temperatures in waters where salinity ranges up to 26 g/L. Drupelets of *R. maritima* s.s. germinate well in water salinities up to 43.4 g/L if an optimum water temperature of 28° C is maintained. These drupelets are very drought-resistant.

Experiments on the germination and growth of wigeongrass from mild climates illustrate the plant's rather complicated life strategy there. Some drupelets germinate at relatively low temperatures (16° C) and the plants grown from them produce flowers and fruit in as little as 8 weeks, whereas plants from drupelets that germinate at a higher rate under optimum temperature (28° C) take up to 5 months to yield fruit. Lack of oxygen—as indicated by low redox potential of –300 mV—retards germination. Thus, in nature, drupelets from plants produced from drupelets that germinate at low spring temperatures probably will easily germinate during summer in places with sufficient oxygen because habitat temperatures will then be near optimum. Drupelets that settle in poorly oxygenated bottoms will lie dormant until the following year. However, drupelets that germinate when optimum temperatures are reached produce plants that do not mature until winter; drupelets from these plants go into winter dormancy, but they germinate in early spring at low relatively low temperatures, starting a new cycle.

Animals also influence germination. Agami and Waisel (1988) found that the hard-seeded drupelets germinated at high rates after passing through the digestive tracts of tilapia (*Oreochromis* sp.) and grass carp (*Ctenopharyngodon idella*). However, nearly all drupelets eaten by common carp (*Cyprinus carpio*) were digested.

I conclude that, although drupelet germination in wigeongrass occurs under a rather narrow range of water levels, drupelets are easily dispersed and adapted to survive and germinate in a wide range of salinity and temperature regimes common to drought-prone environments.

Asexual Reproduction

Ruppia maritima s.l. also colonizes by rhizomes. Rapid growth of rhizomes on overwintering plants begins about the same time as drupelet germination and, like germination, is probably temperature controlled. Colonies reach maximum development dur-

ing July or August in temperate climates. Spring and fall growth peaks occur in subtropical polyhaline estuaries. Recolonization of sediments denuded of wigeongrass by a boat propeller proceeded at about 0.25 m/year (Orth and Moore 1982). Floating fragments of wigeongrass grow roots freely at the nodes, sink, and attach to the bottom. Haag and Noton (1981b) suggested that reproduction of *R. occidentalis* in Alberta wetlands is low under high water conditions when rhizome growth predominates and shoots are short with long leaves. However, they also suggest that lower water levels cause shoots to increase in length and form vegetative propagules (undescribed) that are easily torn from parent plants. Turions (asexual, carbohydrate-rich perennating organs) or turionlike structures have been described on some Australian *Ruppia* taxa by Brock (1982b). These structures are about 2.5 mm long and form terminally on the rhizomes or at the junction of rhizome and leaf sheath. These structures are unknown for *R. maritima* s.s.

Physiology

The distribution, relative abundance, and zonation of communities dominated by wigeongrass and eelgrass (*Zostera marina*) in Chesapeake Bay probably are controlled by underwater light and temperature (Orth et al. 1979). Wetzel and Penhale (1981) and Wetzel et al. (1981) compared the photosynthetic parameters of these two species to directly examine this hypothesis. Wigeongrass was shown to have a higher light and temperature optimum, a shorter growing season, and be photosynthetically less efficient than eelgrass in low levels of underwater light. Wigeongrass was thus considered a "sun" or "high light" plant. The relatively high ratio of chlorophyll *a* to chlorophyll *b* in wigeongrass also suggests that it is less adapted to low-light environments than some of the seagrasses (Evans et al. 1986).

Times of maximum light and temperature may not be in phase and can pose some problems for wigeongrass. Conover (1958) noted that maximum wigeongrass biomass coincided with the slightly lower insolation rates associated with the time of highest water temperature in a Massachusetts estuary. Conversely, in Chesapeake Bay, wigeongrass occurring at sites where light exceeds photosynthetic saturation levels may be temperature-stressed and attain higher

biomass later in the growing season when water temperatures are lower (Wetzel and Penhale 1981). Koch et al. (1974) found that, where algae are present, relatively low light levels can stimulate epiphytes and suppress wigeongrass growth.

Wigeongrass retains some oxygen in the lacunar system for use in respiration, and an oxygen supply to the roots is essential in the anaerobic, highly reducing sediments characteristic of wigeongrass habitat. At such sites, roots can decay from lack of photosynthetically derived oxygen if the supply is reduced by cloaking epiphytes (Richardson 1980). The presence of oxygen-bearing lacunae in the roots would be especially important to allow survival of perennial-behaving populations during dormant periods. An oxygen supply to wigeongrass roots may also help mediate the absorption of phosphorus (P) in anaerobic sediments (Conover 1964a). Culture experiments of Thursby (1984b) show that wigeongrass roots often release oxygen. The resultant nitrification around the root zone probably is not an important source of nitrogen (N), however, as the roots seem best adapted to take up ammonia rather than nitrates or nitrites (Thursby 1983). Instead, the primary function of the oxidized layer may be to reduce the potential for manganese (Mn) or iron (Fe) toxicity or to render harmless the H_2S or other substances found in anaerobic bottoms (Thursby 1984b).

Culture experiments show that wigeongrass leaves and roots take up ammonia and phosphate, but that root-to-shoot translocation predominates (Thursby and Harlin 1984). Uptake of nitrate was negligible when ammonia was supplied to roots. However, sometimes wigeongrass may rely mostly on inorganic nutrients. Pulich (1989) showed with culture experiments that low levels of inorganic nitrogen and phosphorus supplied to wigeongrass by way of the sediments resulted in development of a rhizome system with short shoots, extensive roots, and higher leaf production than with sediments containing high levels of organic nutrients, which produced plants with reduced root biomass, long branching shoots, and lower leaf production. In the same study (Pulich 1989), inorganic nutrients were ineffective in supporting growth of the seagrass *Halodule wrightii*, which required organic nitrogen for vigorous growth. These plants grew in mixed beds in a polyhaline lagoon where the wigeongrass grew most vigorously during cool spring and fall months in sediments low in free H_2S , and the *Halodule wrightii* was most productive during warm summer months on more reduced, organic-rich sediments. Therefore, there is experimen-

tal evidence that differential responses to sediment sulfate reduction are involved in competition between these two species. Thursby (1984a) lists concentrations of major nutrients, vitamins, and trace metals required for long-term culture of wigeongrass.

Wigeongrass effectively uses the HCO_3^- ion as a source of carbon (C; Sand-Jensen and Gordon 1984). At seawater levels of dissolved inorganic C, photosynthesis was highest at pH 7.0–7.5, was maintained at fairly high levels at pH 7.5–9.0, but decreased rapidly to zero at about pH 10.2.

The epidermal leaf cells of wigeongrass probably are modified to absorb both cations and anions for osmoregulation (Jagels 1983; Jagels and Barnabas 1989). This evidence seems to refute Husband and Hickman's (1985) contention that saline conditions are a requirement for maximum growth. Jagels and Barnabas (1989) also stated that wigeongrass likely turns white and dies under conditions of high temperature and widely varying salinity because of the additional energy required for increased osmoregulation. Brock's (1979) hypothesis—that the amino acid proline serves in osmoregulation in wigeongrass—was confirmed by Pulich (1986), who speculated that the substance could also help salinity-stressed plants maintain NH_4^+ levels.

In summary, the known physiological characteristics of wigeongrass support Verhoeven's (1979) contention that the plant has little competitive strength outside its rather well defined ecological niche. The plant adapts poorly to dimly lit waters or anaerobic sediments but has specialized features enabling survival under varying salinities and high temperature beyond those tolerated by other submersed angiosperms. Although most of the physiological evidence comes from in vitro experiments, it seems evident that, to produce large amounts of wigeongrass, managers must provide shallow, clear waters and probably expect significantly lower production from (1) relatively small increases in turbidity or (2) lower temperatures because of excessive water depth. Problems with epiphytic algae may also occur in highly fertile waters.

Growth and Production

Rate

Wigeongrass in southwest Canada can germinate and produce mature drupelets in about 2 months

(Harrison 1982), whereas, in southern France, other annual-behaving plants take as long as 5 months to mature (Van Vierssen et al. 1984). In climates where spring and fall growth peaks occur, plants probably grow faster in the spring (Pulich 1989). I found no information about the rates at which wigeongrass stems, leaves, or rhizomes elongate in nature.

Yield

Vegetation

Healthy stands of wigeongrass usually contain about 500–1,500 stems or plants per square meter (McMahan 1969; Corell et al. 1978a, 1978b; Keddy 1987), but densities up to 5,376/m² occur (Anderson 1966). Plants in fine sediments probably achieve greater densities than those in coarse sediments (Conover and Gough 1966).

Annual *Ruppia* taxa may be less productive than perennials because the former usually occur in wetlands subject to high salinities, desiccation, and other stresses (Verhoeven 1980b; Brock 1982b). Conover (1958) and Evans et al. (1986) found that, in a temperate climate, perennial-like wigeongrass had a single peak of aboveground biomass in midsummer. The peak can occur in early fall at shallow sites where plants are temperature-stressed and photoinhibited (Wetzel et al. 1981). Standing crop can peak nearly a month after the period of maximum growth rate (Wetzel 1964). Orth and Moore (1988) found a strong correlation between percent cover and wigeongrass biomass in Chesapeake Bay. Distinct spring and fall growth periods are usual for wigeongrass in the southern United States, and great midsummer reductions in wigeongrass biomass or even complete die-offs are sometimes seen (Joanen and Glasgow 1965; Percival et al. 1970; Swiderek 1982). Flores-Verdugo et al. (1988) found winter and summer biomass peaks for wigeongrass in a tropical Mexican lagoon. They suggested that the scarcity of wigeongrass during the wet season (July to October) probably was the result of nutrient inflows from a river, which led to stimulated phytoplankton growth and increased turbidity.

Biomasses of *Ruppia* taxa from around the world are compared in Table 2. The highest *Ruppia* biomass yet recorded (1,748 g/m² dry weight) occurred for the perennial *R. megacarpa* in fine-textured sediments in the shallowest (<1 m) portions of a brackish (salinity about 20 g/L) southern Australian

Table 2. *Ruppia spp.* maximum biomasses and probable factors limiting biomass.^a

Reference	Total or aboveground biomass (g/m ² dry weight) ^b	Code to limiting factors ^c															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Reed 1979	2.0	x			x												
Gibbs 1973	2.7		x	x													
Davis and Carey 1981	3.1	x	x	x													
Stieglitz 1966	3.9	(none indicated)															
Harrison 1982	4.0		x														
Getsinger et al. 1982	9.6	x		x													
Ankar and Elmgren 1977	15	(none indicated)															
Jemison and Chabreck 1962	20	(none indicated)															
Conover 1958	24													x		x	
Prevost et al. 1978	25			x													
Jerling and Lindhe 1977	25		x			x											
Kiorboe 1980	28													x			
Van Vierssen 1982a	28		x														
Zimmerman and Livingston 1979	34	x	x	x													
Jensen 1940	43	x	x							x							
Gidden 1965, unpublished data	43	x				x			x							x	
Correll et al. 1978a	49	(none indicated)															
Orth and Moore 1988	55	x		x													
Wetzel 1964	64																x
Schuler 1987	64	(none indicated)															
Thorne-Miller et al. 1983	80		x	x					x								
Orth and Moore 1982	91		x														
Bailey and Titman 1984	96	(none indicated)															
Muus 1967 in Verhoeven 1980b	100	(not seen)															
Swiderek 1982	120				x		x	x									
Pulich 1985	160		x				x										
Harlin and Thorne-Miller 1981	190			x													
Singleton 1951	197	(none indicated)															
Heitzman 1978	197	(none indicated)															
Grontved 1958	234	(none indicated)															
Orth and Moore 1982	236	(none indicated)															
Gonzalez-Gutierrez 1977																	
in Verhoeven 1980b	253	(not seen)															
Joanen 1964; Joanen and Glasgow 1965	282	x		x		x				x	x	x					
Davis et al. 1985	291	(none indicated)															
Verhoeven 1980b	386	x		x								x					
Brock 1982b	410	(none indicated)															
Congdon and McComb 1979, 1981	503	x			x				x				x				
Flores-Verdugo et al. 1988	620	x		x									x	x			
Higginson 1967 in Congdon and McComb 1979, 1981	700				x				x								
Anderson 1966	800	(none indicated)															
Edwards 1978	1,000	(none indicated)															
Nixon and Oviatt 1973	1,460	(none indicated)															
Lukatelich et al. 1987	1,748					x			x						x		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16

^a Limiting factors in some cases apply to lower biomasses than listed.^b Water displacement volume (mL) conversion to dry weight: multiply by 0.111. Ash-free dry weight conversion to dry weight: multiply by 1.33. Fresh weight conversion to dry weight: multiply by 0.15.^c Codes: 1 = Excess turbidity or color; 2 = Competition by angiosperms; 3 = Competition by macroalgae or phytoplankton; 4 = Excess wave action; 5 = Excess water depth; 6 = High water temperatures; 7 = Excess water salinity; 8 = Excessively coarse sediments; 9 = Water level fluctuations; 10 = Excess sediment salinity; 11 = Excessive consumption by birds; 12 = Excess water currents; 13 = Epiphytes; 14 = Insufficient water column nutrients; 15 = Excessively soft sediments; 16 = Insufficient insolation.

estuary receiving significant amounts of N and P from agricultural runoff. The highest *R. maritima* bio-mass (1,460 g/m² dry weight) was from a shallow (0.10–0.50 m), warm (32–33° C in June), well insolated and fertile Rhode Island embayment, where salinities ranged from 20 to 22 g/L and bottom sediments were extremely rich in organic matter (36–58% in the upper 5 cm; Nixon and Oviatt 1973). *Ruppia maritima* biomass up to 1,000 g/m² dry weight occurred in a shallow Mexican lagoon that also contained large amounts of organic matter in the sediment (Edwards 1978). Verhoeven (1980b) believed that, under ideal circumstances, the largest standing crop possible for European *Ruppia* taxa was about 400 g/m² dry weight, and he suggested that an American taxon might be more vigorous.

Peak recorded *Ruppia* biomasses <400 g/m² dry weight are common. The most common factors associated with these low biomasses are excessive turbidity, competition (most likely for light) by other angiosperms or algae, and excessive wave action or water depth. Filamentous algae can inhibit *Ruppia* production by shading and by entanglement, which causes plants to be more sensitive to wave action (Verhoeven 1980a).

Despite the negative effects of shading and entanglement, algal mats may benefit wigeongrass in some circumstances. Richardson (1980) found that partial shading by algal mats reduces epiphyte fouling on wigeongrass. He also noticed that algal mats in dried wetlands hold water, which may increase the survival of wigeongrass lying under the mats. Other factors that frequently are suspected to cause low *Ruppia* biomass are high water temperatures, excessive salinity, overly coarse or soft sediments, and "eatouts" by waterfowl.

Propagules

McMillan (1985) found a maximum density of 4,110 wigeongrass drupelets per square meter in a Texas lagoon. There is no information on the total number of drupelets produced in a season by a single wigeongrass plant.

Wetlands managed for wigeongrass production can produce >6.6 g/m² dry weight of drupelets (Swiderek 1982). In waterfowl exclosures, Prevost et al. (1978) found the dry weight of drupelets in sediments to be nearly twice that annually produced; this suggested that drupelets can persist into succeeding growing seasons.

Chemical and Caloric Content

Dry matter composes 10–17.47% of the fresh weight of wigeongrass (Lindstrom and Sandstrom 1938; Vicars 1976; Reed 1979). Leaves contain about 15.8% dry matter and the root system about 11.5% (Wetzel et al. 1981). Vicars (1976) gave the oven-dry weight as 71.6–81.9% of dry weight. Ash content varies from 15.9 to 42.0% of dry weight (Lindstrom and Sandstrom 1938; Reed 1979), but this measurement depends on how efficiently calcareous encrustations and other matter are removed from the plants. Plants analyzed by Reed (1979) had highest ash content (42% of dry weight) in spring. Kiorboe (1980) considered the ash-free aboveground and belowground dry weights to be 84% and 77%, respectively, of total dry weights. Verhoeven (1980b) used 25% as an average figure to convert dry weight biomass to ash-free biomass. The dry weight of fresh wigeongrass required to displace 1 mL of water averages 0.111 g (C. S. Gidden, 1965, unpublished data).

Gross energy of wigeongrass is 3.2–3.6 Kcal/g dry weight (Nixon and Oviatt 1973; Paulus 1982). Mean annual caloric content of leaves and rhizomes measured by Walsh and Grow (1972) was 4.44 and 4.25 Kcal/g ash-free dry weight, respectively.

Protein content of wigeongrass varies from 5.2 to 21.9% of dry weight (Christensen 1938; Lindstrom and Sandstrom 1938; Paulus 1982; Swiderek 1982). The annual mean protein content of leaves and rhizomes, respectively, is 23.2% and 20.0% of the ash-free dry weight (Walsh and Grow 1972). Grøntved (1958) calculated that the standing crop of *Ruppia* in a Danish fjord contained about 25 g/m² albumen.

Lipid content in dry matter of South Carolina wigeongrass was 1.5% (Swiderek 1982). Attaway et al. (1970) found that lipids compose 2.5% of the dry weight, nonsaponifiable material 1.0%, and hydrocarbons 0.073%. All these figures are much higher than those found in four seagrasses collected nearby. They postulated that the absence of short-chain hydrocarbons (C₁₅–C₂₂) in *Ruppia* may chemically distinguish the family Ruppiaceae from the Zannichelliaceae and Hydrocharitaceae and strengthen Hutchinson's (1959) taxonomic treatment of the seagrasses. A later analysis of the sterols in a sample of wigeongrass that contained 2.2% dry weight lipids revealed the species to be peculiar (when compared to four seagrasses) in its relatively high content of campesterol (Attaway et al. 1971). Analyses of Rhode Island wigeongrass by Jeffries

(1972) showed that it contains a variety of C_{16-18} fatty acids. Parker (1964) measured ratios of stable C isotopes in Redfish Bay, Texas, wigeongrass to test their potential usefulness in determining food chain patterns.

Annual mean carbohydrate content of wigeongrass leaves and rhizomes is 27.0% and 63.6% of the ash-free dry weight, respectively (Walsh and Grow 1972). The more soluble carbohydrates composed 35.1% of the dry matter in samples analyzed by Swiderek (1982). Cellulose and starch contents are 16.4% and 3.04% of oven-dry weight, respectively (Lindstrom and Sandstrom 1938). Crude fiber content is 16.5–16.9% of dry weight (Paulus 1982; Swiderek 1982).

Wigeongrass can remove large amounts of N and inorganic P from the water column (Twilley et al. 1981). Thursby (1984a) considered dry leaf tissue content of 2.5–3.0% N and 0.25–0.35% P to indicate the minimum amounts required for optimal wigeongrass growth. Vicars (1976) showed that wigeongrass from shallow sites had lower N (1.77 mg atomic N/g ash-free dry weight) and P (0.19 mg atomic P/g ash-free dry weight) content than plants gathered from deeper sites. McKay (1934) compared the cell liquid of wigeongrass to the highly concentrated $MgSO_4$ waters where the plants grew and found lower concentrations of magnesium (Mg), sulfate, and sodium (Na) in the plant tissue than in the water. The opposite was true for the major nutrients (N, P, and potassium [K]), as well as for calcium (Ca) and chlorine (Cl). Verhoeven (1979) found that the K and Mg content of *R. maritima* s.s. did not relate to the environmental concentrations of these elements but that the Ca and Na concentrations did. In addition, he found the concentrations of these elements well within the ranges listed by Hutchinson (1975) for freshwater macrophytes.

Nutrient (N, P, K) concentrations in aboveground versus belowground portions of wigeongrass have been compared in several studies (Walsh and Grow 1972; Wetzel et al. 1981; Getsinger et al. 1982; Van Vierssen 1982b; Pulich 1989). With the possible exception of K, these nutrients are generally in greater concentrations in aboveground parts. Pulich (1989) noted that, in fall, P content of roots slightly exceeds that of leaves. His experiments suggested that leaves are the major nutrient sink in wigeongrass and that water-column nutrients are used through the leaves.

Little information is available for the minor nutrients. Walsh and Grow (1972) found greater Mn concentrations in aboveground than belowground

material, in contrast to the results of Van Vierssen (1982b). Negligible differences in aboveground versus belowground concentrations of Na, Ca, Mg, or Fe were noted by Van Vierssen (1982b).

The elemental composition of wigeongrass is shown in Table 3. Information is also available on concentrations of other elements found in wigeongrass vegetation growing in irrigation drainwater evaporation ponds in California (Schuler 1987; Schroeder et al. 1988). Schuler (1987) also lists selenium (Se) and boron (B) concentrations in wigeongrass drupelets from this area. In sufficient quantities, these two elements are potentially toxic to waterfowl.

In summary, available information on the chemical composition of wigeongrass provides few clues about why the plant is such an important waterfowl food. Protein, carbohydrate, and lipid content of aboveground parts is slightly higher than in sago pondweed, which is also heavily used by feeding waterfowl, but mostly for its carbohydrate-rich turions (Kantrud 1990). Several other common submersed macrophytes have higher contents of these nutrients in aboveground parts than wigeongrass (Paullin 1973), but they rank much lower as waterfowl food. Perhaps the delicate texture of wigeongrass leaves and stems adds to the plant's palatability. Very little is known about the chemical composition of wigeongrass drupelets.

Decomposition

Decomposing wigeongrass beds are an important source of organic matter in some estuarine ecosystems (Tenore 1972). Taller stands in temperate climates begin decomposing at stem bases after about 3 months of exponential growth, which leads to wind "mowing" and the movement of large amounts of plant material to shore. Stunted plants in more inhospitable habitats die from desiccation or salinity or are removed from bottom sediments by water turbulence or feeding waterfowl (Verhoeven 1979). Major shoreward movement of detached wigeongrass stems and leaves in late summer can coincide with peak populations of epiphytes and animal grazers (Conover 1958). Verhoeven (1978) estimated that about 44% of the fall decrease in biomass of *Ruppia cirrhosa* was attributable to leaching and decomposition and the remainder to grazing by birds and invertebrates. Litter bag experiments show that grazing by macroinvertebrates (*Gammarus* sp. and *Sphaeroma*

Table 3. Elemental composition of whole plants or aboveground vegetation of wigeongrass (*Ruppia maritima*).

Element	Unit of measure ^a	Range or single observation (reference ^b)
Aluminum (Al)	%	0.64 (6)
Barium (Ba)	ppm	9.1 (6)
Boron (B)	ppm	265.1 (6)
Carbon (C)	%	32.7 (1)
Calcium (Ca)	%	0.28 (2)–2.45 (3)
Cadmium (Cd)	ppm	0.5 (6)
Cobalt (Co)	ppm	34.6 (6)
Chromium (Cr)	ppm	2.6 (6)
Copper (Cu)	ppm	7.3 (6)
Iron (Fe)	%	0.04 (2)–0.18 (4)
Potassium (K)	%	0.85 (4)–4.59 (2)
Magnesium (Mg)	%	0.44 (5)–1.27 (4)
Manganese (Mn)	%	0.002 (4)–0.62 (2)
Nitrogen (N)	%	1.37 (1)–2.94 (2)
Sodium (Na)	%	0.35 (3)–3.38 (2)
Nickel (Ni)	ppm	2.17 (6)
Phosphorus (P)	%	0.12 (5)–1.02 (2)
Lead (Pb)	ppm	17.5 (6)
Strontium (Sr)	ppm	80.16 (6)
Zinc (Zn)	ppm	10.0 – 30.0 (4)

^a Measurements refer to dry matter.

^b Reference: 1—Twilley et al. 1986; 2—Van Vierssen 1982b; 3—Verhoeven 1979; 4—Walsh and Grow 1972; 5—Getsinger et al. 1982; 6—Swiderek 1982.

sp.) reduces leaves and shoots of *Ruppia cirrhosa* to particles of <1 mm in 180 days (Menendez et al. 1989).

In North Carolina impoundments, wigeongrass begins to turn yellow and deteriorate during the hot summer months, but plants recover by fall (Heitzman 1978). Such fall growth does not rapidly decompose, and October-flowering plants can still be used by waterfowl in January.

Indoor cultures of *R. maritima* were kept in darkness at 20° C in aerated estuarine water and lost 50% mass in 35 days; after 93 days, they showed slightly elevated C and N concentrations and slightly lower amounts of P (Twilley et al. 1986).

Senescence and detachment of stems from the belowground parts of wigeongrass can coincide with an increase in H_2S bacteria on the plants and in the substrate (Richardson 1980). Sediment sulfate reduction activity may be an important factor regulating the decrease in wigeongrass and increase in the seagrass *Halodule wrightii* in subtropical lagoons during hot summer months (Pulich 1989).

Habitat and Associated Abiotic Limiting Factors

The range of physical conditions in wetlands supporting wigeongrass is given in this section with the realization that current environmental conditions may be poor indicators of habitat suitability. Adult plants can tolerate much harsher conditions than those required for germination or early growth, and, as suggested for *Potamogeton pectinatus* (Van Wijk et al. 1988), genetically different populations, able to reproduce in local, highly stressful environments, may have evolved.

Wetland Type

Ruppia maritima s.l. occurs mostly in coastal bays (temporarily to permanently flooded and mesohaline to hypersaline); estuaries, fjords, lagoons, ponds, pannes, and sounds; and in bayous, creeks, ditches,

flats, and rivers subject to tidal influence (Olsen 1945; Millard and Scott 1953; Thorne 1954; Ferguson-Wood 1959; Kornas et al. 1960; Phillips 1960b; Hyer 1963; Joanen 1964; Joanen and Glasgow 1965; Verhoeven 1979, 1980a; Richardson 1980; Thorne-Miller et al. 1983; Ferren 1985). Verhoeven (1979) defined temporary water bodies for wigeongrass as those where physical conditions do not allow survival of vegetative plant parts during certain periods of the year.

In tidal estuaries, wigeongrass usually occurs at elevations between mean lower low water and mean higher low water (McNulty et al. 1972; Jefferson 1974). The species also mixes with true seagrasses up to at least 1.5 km offshore in large oceanic bays (e.g., the Gulf of Mexico; Zimmerman and Livingston 1979). Wigeongrass is often propagated in coastal impoundments in the United States because it is attractive to waterfowl (Davis et al. 1985). For example, Tiner (1977) showed that nearly 7,500 ha of such impoundments exist in a single South Carolina estuary. Daiber (1974) cited several references showing that impoundments built to increase production of salt marsh hay have also created wigeongrass habitat in the eastern United States. Prolific stands of wigeongrass also occur in muskrat "eat-outs" and alligator holes in wetlands along the Gulf of Mexico (Bateman et al. 1988).

In noncoastal waters, wigeongrass occurs in fresh to hypersaline, palustrine and lacustrine wetlands (Metcalf 1931; Moyle 1945; Stewart and Kantrud 1971, 1972; Reynolds and Reynolds 1975; McCarraher 1977; Pip 1979) as well as in mound springs and artesian bores (Jacobs and Brock 1982). Of 17 reported occurrences of wigeongrass in south-central Canada, Pip (1979) found 82% in lakes, 12% in ponds, and 6% in creeks.

Wetland Area and Fetch

Wigeongrass in Rhode Island showed greater coverage of small ponds (<1.3 ha) than in larger water bodies where plants occurred only around shorelines and in coves (Wright et al. 1949). Extensive surveys of Louisiana wetlands showed that few submersed macrophytes of any kind grow in lakes >2.59 km², probably because of excessive depth and wave-induced turbidity (Chabreck 1972). Breuer (1961 in Cornelius 1975) and McMahan (1969) found wigeongrass relatively unimportant in the huge Laguna Madre of Texas, where the plant occurred

only around protected areas. South along the Mexican Gulf Coast, however, a mixed bed of wigeongrass and *Najas* occupied about half of the 1,000-km² Laguna Tamiahua; other extensive stands also grew in large interior lakes and Pacific Coast lagoons in that country (Saunders and Saunders 1981). Pip (1979) found 82% of Canadian wigeongrass occurrences in lakes >10 ha. Nearly the entire bottom of a shallow (<1 m), 94-ha saline lake in central North Dakota was a wigeongrass monotype for at least 3 years (H. A. Kantrud, personal observation).

Water Column

Depth

Wigeongrass occurrence spans a water depth of 0–4.5 m (Table 4). Kornas et al. (1960) found the highest frequency of wigeongrass at 2–4 m in a brackish bay, but the "richest" stand occurred at only 0.4 m. Joanen (1964) and Joanen and Glasgow (1965) saw the largest biomass in waters 0.6 m deep in the field but, under optimum growth conditions in the laboratory, most growth occurred at 0.4 m. Harwood (1975), however, found the density of wigeongrass to be independent of depth within estuarine waters 0.4–1.3 m deep.

The depth that wigeongrass will grow in any particular wetland seems more strongly related to particle size of bottom substrate than depth per se. No wigeongrass occurred on clays or silts at depths >1.5 m, but plants were several times recorded on sand in waters >2.0 m deep (Table 4). Similarly, optimum wigeongrass growth in clay-bottomed wetlands was not reported at depths >0.61 m, whereas lush growths in sandy-bottomed wetlands were noted at depths up to 4.0 m. In Chesapeake Bay, United States, depth distribution of wigeongrass was +20 to –100 cm (relative to mean low water) in the relatively clean eastern shore waters compared to +10 to –80 cm along the more turbid western shore (Orth and Moore 1988). Thus it is likely that the susceptibility of bottom substrate to wind-induced turbidity often governs the depth distribution of wigeongrass.

Depth, in addition to sediment chemistry and water level fluctuation, influences the growth habit of wigeongrass. Plants from shallow pannes exhibited a procumbent habit with distinctly forking stems and short internodal lengths (Fig. 2), but plants from deeper waters (Fig. 3) were more ascending and had

Table 4. *General habitat features for wigeongrass (Ruppia maritima) arranged according to increasing observed tolerance of water depth.*

Depth (m) ^a		Water turbidity	Water salinity	Predominant substrate texture	Reference
Range or single observation	Optimum ^b				
0.05–0.10			mixosaline		Verhoeven and Van Vierssen 1978a
0.15				sand	Van Vierssen 1982a
0.0–0.3					Verhoeven 1975
0.1–0.3				organic	Nixon and Oviatt 1973
0.06–0.37	0.18		mixosaline		Chabreck 1960
<0.3					Miller and Egler 1950
<0.4			mixosaline	clay	Verhoeven 1979
0.30–0.45					Gilmore et al. 1982
0.15–0.46			mixosaline	loam	Montz 1978
0.28–0.48					Singleton 1951
0.05–0.5			mixosaline	sand, shell	Pulich 1985
<0.5			mixo–hypersaline		Hammer and Heseltine 1988
0.5			mixo–hypersaline		Sullivan 1977
0.29–0.55	0.36–0.56	little	mixosaline	clay	Schuler 1987
0.05–0.6			mixosaline	organic	Heitzman 1978
0.1–0.6					Richardson 1980
0.3–0.6		little	mixosaline	clay	Swiderek 1982
			hypersaline	clay	H. A. Kantrud, unpublished data
0.6			mixosaline		Harlin and Thorne–Miller 1981
0.0–0.61			mixosaline	clay	Nelson 1954
0.05–0.61	0.61	moderate	mixosaline	clay	Joanen and Glasgow 1965
0.08–0.61		little	hypersaline		Davis and Tomlinson 1974
0.61			mixosaline		Neely 1962
0.2–0.7			mixosaline		Koch and Seeliger 1988
0.3–0.7					McCarragher 1977
<0.7	0.53				Christian 1981
<0.7		limiting	mixosaline	organic clay	Verhoeven 1979
0.1–0.75	0.1–0.3		mixosaline		Lindner 1978
0.03–0.77	0.2–0.65	moderate	mixosaline		Mahaffy 1987
<0.8	0.2–0.4		mixosaline	sand	Orth et al. 1979
	0.46–0.91				Beter 1957
<0.91	<0.61		mixosaline	muddy sand	Scott et al. 1952
<0.91				mud	Eleuterius 1971
<1.0					Congdon and McComb 1979
<1.0			mixosaline	silt	Koch et al. 1974
<1.0			mixosaline		Orth and Moore 1988
1.0			fresh–hypersaline	mud	Flores–Verdugo et al. 1988
0.0–1.0	0.0–0.5				Wetzel et al. 1981
0.2–1.0	0.2–0.6				Muus 1967
	1.0			sand	Tenore 1972
0.33–1.0			polysaline–hypersaline		Hellier 1962
<0.61–1.19	0.91–1.04				Sincock 1965, unpublished data
0.3–1.2	0.6–0.7	moderate	mixosaline		Reed 1979
<1.2			mixosaline	sand	Verhoeven 1979
1.22			mixosaline	muck	Oberholzer and McAtee 1920

Table 4. *Continued.*

Depth (m) ^a		Water turbidity	Water salinity	Predominant substrate texture	Reference
Range or single observation	Optimum ^b				
0.4–1.3			mixosaline		Harwood 1975
0.1–1.5			hypersaline	silt, shell, marl	Davis 1978
<1.5					Geddes et al. 1981
>1.5				silty clay	Carter et al. 1985
<1.6			mixosaline		Reynolds and Reynolds 1975
<1.73					Keddy 1987
0.8–1.8			mixosaline	sand, organic	Thorne–Miller et al. 1983
<1.83			mixosaline		Wright et al. 1949
<1.83					Ferguson Wood 1959
<1.83					Wood 1959
	<1.83				Holmes 1972
0.5–2.0			mixosaline	mud	Klavestad 1957
0.6–2.0	0.8–1.0				Davis and Carey 1981
1.0–2.0		little	mixosaline	sand, mud	Getsinger et al. 1982
<2.0					Zimmerman et al. 1979
<2.0	<1.5		mixosaline		Zimmerman and Livingston 1979
<2.0			mixosaline		Armstrong and Anderson 1966
<2.0				sand	Grontved 1958
>2.0					Chapman 1960
<2.13	1.52		mixosaline	“soft”	Conover 1961
0.61–2.13	0.61–1.52		mixosaline	shell, muddy sand	Phillips 1960a
1.9–2.9			mixosaline	sand	Harrison 1982
0.6–3.0					Weldon et al. 1969
3.0				sand	Neel et al. 1973
<3.05		moderate	mixosaline		Brannon 1911
>3.05					McAtee 1935
0.1–3.50.1					Congdon and McComb 1981
0.25–3.5	0.0–1.9	little	mixosaline	sand	Haag and Noton 1981a
0.0–4.0	0.0–1.0				Olsen 1945
<4.0					Crum and Bachmann 1973
<4.0	0.8–3.0				Husband and Hickman 1985
0.4–4.5	2.0–4.0		mixosaline	sand	Kornas et al. 1960
1.0–4.5	1.0–3.5		fresh	sand	Haag and Noton 1981b

^aDepths in tidal areas relative to mean low water (MLW; e.g., –1.0 m MLW = 1.0 m); depths above MLW not shown.

^bOptimum depths as stated by author; or where maximum biomass or frequency was shown in tables or graphs; or where best propagation results were obtained.



Fig. 2. Elongate life form of *Ruppia maritima* as a result of growth in deeper waters. Longer internodes between branches are typical.

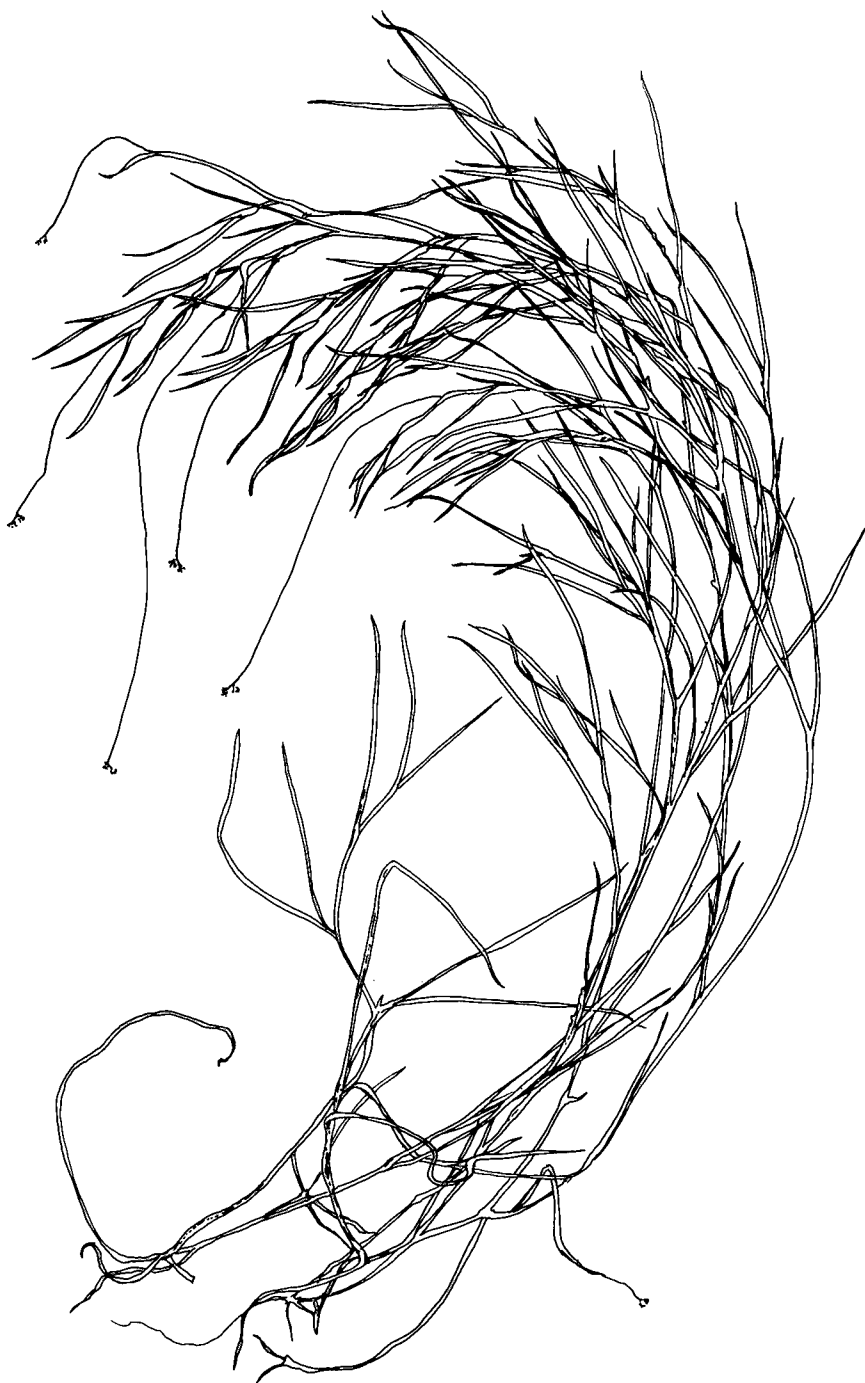


Fig. 3. In shallow waters *Ruppia maritima* shows a more compact growth form with pronounced forking of stems and short internodes.

longer internodes (Richardson 1980). In shallow sites, plants adjusted to the stress of high light and temperature by concentrating leaf area in the lower portion of the canopy (Wetzel et al. 1981).

Transparency

As mentioned earlier, wigeongrass requires much sunlight. Verhoeven (1979) believed wigeongrass could only develop normally in clear water and always found the species greatly reduced or absent in water turbid from suspended materials. Water stained with dissolved organic materials, especially from woody plants, can also reduce water transparency in managed wigeongrass impoundments (Heitzman 1978).

Large beds of wigeongrass have disappeared as a result of a rapid increase in turbidity (Anderson 1970). Joenen (1964) and Joenen and Glasgow (1965) found that turbidity was most harmful to young plants and recommended that wetlands managed for wigeongrass have <25–55 ppm turbidity. Gore (1965) found wigeongrass in waters with 17.5–42.5 ppm turbidity. According to Day (1952), a Secchi disk reading of 1 m equals about 185 ppm suspended solids. A saline wetland in Alberta, Canada, where wigeongrass was the dominant macrophyte, had relatively high water transparency (Secchi 3.0 m; extinction coefficient 0.8), low phytoplankton productivity, and a large standing crop of benthic algae (Gallup 1978). Wigeongrass biomass decreased markedly when Secchi depth decreased to <1 m concurrent with a decrease in water levels (Bailey and Titman 1984). Zimmerman and Livingston (1979) found wigeongrass where turbidities reached 120 Jackson turbidity units (JTU), but the plant was one of the three major dominants only where turbidities were <60 JTU. They also found the plant where color was 0–570 platinum-cobalt units (PCU), but most growth was in waters with <370 PCU.

Tidal waters with dense wigeongrass populations, examined by Richardson (1980), were usually clear during the growing season but occasionally became turbid from climatic events or flooding. However, those with sparse growths were frequently to consistently turbid due to dissolved organic matter, organic and inorganic particulates, or living phytoplankton and zooplankton. Harwood (1975) noted that storm-induced turbidity can limit growth of wigeongrass.

A 40% reduction in light intensity gave a 50% reduction in wigeongrass standing crop during shading experiments of Congdon and McComb (1979).

They suggested that, in tidal wetlands, reduced light intensity is an important factor limiting the area where wigeongrass can grow because plants die from overexposure to air at shallow sites where light is not limiting. In some areas, poor insolation due to fog, mountains, or short days can be the main cause of reduced wigeongrass production (Wetzel 1964). Short periods of high turbidity probably are not harmful to wigeongrass, as Millard and Scott (1953) found that the plant prospered in shallow, sometimes exposed sites, where Secchi disk readings sometimes fell to <7 cm. In the production of high turbidity, Conover (1964a) considered winds that roil bottom sediments and detritus in shallow wigeongrass lagoons to be more important than living planktonic algae. Established stands of wigeongrass do not always increase as turbidity decreases. Thorne-Miller et al. (1983) reported a decline in wigeongrass following breachway construction from the ocean to a coastal lagoon. Secchi transparency increased to at least 2.3 m, allowing *Zostera marina* to become dominant. However, they noted that other important factors—such as increased water circulation and salinity—could have caused the wigeongrass decline.

The stimulatory effect of nutrient enrichment from sewage and agricultural runoff on phytoplankton probably is the main cause of man-made turbidity in areas (e.g., Chesapeake Bay, where wigeongrass and other submersed macrophytes have declined; Carter et al. 1985). I found only a single case where industrial contaminants may have been implicated: in Florida, pulp mill wastes caused noticeable increases in turbidity and color up to 5 km from estuarine mouths, restricting wigeongrass to sites >1.4 km offshore even though competition with true seagrasses and large marine algae was greater there (Zimmerman and Livingston 1979). However, higher levels of dissolved P, biochemical oxygen demand, and chemical oxygen demand were also found in the area where wigeongrass was absent.

To summarize, the relatively shallow waters inhabited by wigeongrass, its photosynthetic and physiological parameters, and its negative response to small increases in turbidity show that control of water transparency is of utmost importance to establish and maintain stands.

Water Chemistry

The genus *Ruppia* tolerates a wider range of water salinity than any other group of submersed angio-

sperm (Brock 1979). Table 5 shows that *Ruppia maritima* s.l. occurs in waters containing 0.6–390 g/L.

Joanen and Glasgow (1965) found no differences in wigeongrass growth in Louisiana waters that ranged from 3.7 to 33.4 g/L salinity. The upper limit slightly exceeds sea strength (about 32 g/L). The plant was one of the few angiosperms able to grow in both hypo- and hypersaline areas in Texas lagoons, where waters ranged from nearly fresh to over 60 g/L (Conover 1964b). Nevertheless, wigeongrass can become restricted to peripheral areas when breachway construction between the ocean and closed lagoons allows inflows of water at full sea-strength (Thorne-Miller et al. 1983). Sometimes, however, such breachways can result in increases in wigeongrass if dilution of hypersaline waters occurs (Breuer 1962). Wigeongrass in a Florida bay (maximum salinity 27.7 g/L) reached maximum abundance in July when yearly salinity was minimum (13.2–14.7 g/L). In another year, the salinity fell to 5–10 g/L, nearly eliminating the wigeongrass, but stimulating dense growths of muskgrass (*Chara* spp.; Tabb et al. 1962). Saunders and Saunders (1981) recorded no wigeongrass, but abundant marine algae, in a Mexican lagoon when salinity was about 16 g/L. Wigeongrass first appeared during the year that salinity fell to 10.5 g/L, and maximum development of stands occurred during a year when salinity was about 6.4 g/L. Wood (1959) and Strawn (1961) also noted the affinity of wigeongrass for low-salinity ocean water.

Wigeongrass tolerates extremely high salinities (up to 390 g/L) in lakes where MgSO_4 is the principal salt (St. John and Courtney 1924; Woronichin 1926). Verhoeven (1979) pointed out that the osmotic effect of such high MgSO_4 concentrations is equivalent to NaCl salinities half as high and cited Bourn's (1935) work that suggested NaCl was more toxic to wigeongrass than other salts at the same osmotic concentration. Millard and Scott (1953) saw beds of wigeongrass regularly die back in a South African estuary when chlorinities exceeded 38 g/L (salinity 69 g/L). Such plants, presumably behaving as perennials, survived for at least 2 months in seawater evaporated nearly to the point of crystallization (chlorinity 198 g/L; salinity 358 g/L).

Ruppia maritima s.l. also grows in a wide range of salinities in the prairie pothole region of interior North America. Stewart and Kantrud (1972) found wigeongrass in wetlands that ranged from 0.35 to >100 g/L and listed the *maritima* variety as abundant at 15 to >100 g/L. Metcalf (1931) found wigeongrass fruiting abundantly in prairie wetlands with salini-

ties up to 36 g/L. Millar (1976) listed 15–>45 g/L as the normal salinity of waters supporting wigeongrass in prairie Canada. In this region and the prairies of the northern United States, the *occidentalis* variety, sometimes called "western wigeongrass," is found in deeper waters (up to 2 m) with salinities up to about 18 g/L (Stewart and Kantrud 1971; Anderson and Jones 1976; Larson 1979). This inland variety, probably perennial from quiescent rhizomes, is also found across the northern part of the contiguous United States of America, southern Canada, and Alaska (Pip 1978; Larson 1979; Brayshaw 1985). Although it occurs in waters with as little as 60 mg/L total dissolved solids (TDS), the plant mostly inhabits waters with higher than average salinity (Pip 1979). Husband and Hickman (1989) suggested that the effects of salinity on the colonization of new sites, rather than on the performance of the plant within sites, may be the most important factor determining the distributional limits of this species in Alberta wetlands.

In southern Australia, perennial *Ruppia* taxa occupied deeper, permanent waters with salinities 12–50 g/L; annual types inhabited shallow, less permanent wetlands with salinities up to 230 g/L (Brock 1982a, 1982b). In the ephemeral lakes of western Australia, Geddes et al. (1981) found wigeongrass growing in waters of 3.7–78.3 g/L TDS, but at 81.7–142.0 g/L, only drupelets occurred.

Early in the growing season, wigeongrass with annual growth habit seems to have an affinity for areas with low salinity (Richardson 1980). Salinity may control fruit size and shape, and fruit produced in early summer can have a thicker coat than that from the same plant in early fall (Mayer and Low 1970; McMillan 1974).

Ruppia maritima s.l. has often been cultured to determine the effects of salinity. Best growth occurred at 4.7–22.6 g/L (Joanen 1964; Joanen and Glasgow 1965). Plants flower at 1.8–28 g/L (Bourn 1935; Mayer and Low 1970; McMillan 1974; McRoy and McMillan 1977; Verhoeven 1979) and grow at up to 70 g/L (McMillan and Moseley 1967). Mayer and Low (1970) found that 6-week-old plants tolerated higher salinity (27 g/L) than 8- and 12-week-old plants (21 g/L). Thursby (1984a) grew wigeongrass in liquid media and found the most growth at 10 g/L in both natural and artificial seawater; drupelets germinated in about 6 weeks at this salinity. Drupelets were not produced in seawater concentrated to 52.5 g/L by Bourn (1935). Ortu (1969) noted that drupelets immersed in a solution

Table 5. *Salinities of waters supporting wigeongrass (Ruppia maritima), arranged according to increasing maximum observed salt tolerance.*

Salinity or total dissolved solids (mg/L) ^a		Dominant cation(s)	Reference
Range or single observation	Optimum		
454		SO ₄	Gladyshev and Kogan 1977
60–2,108			Pip 1979
175–2,165		HCO ₃	Haag and Noton 1981b
2,165			Haag and Noton 1981a <i>in</i> Husband and Hickman 1989
1,870–2,760		Cl	Bolen 1964
500–3,000		Cl	Brock and Lane 1983
1,050–3,000		HCO ₃	Reynolds and Reynolds 1975
3,000		SO ₄	Reynolds and Reynolds 1975
140–3,100	668		Disrud 1968
2,000–5,000		Cl	Getsinger et al. 1982
5,000		Cl	Verhoeven and Vierssen 1978a
3,000–5,000		Cl	Ungar et al. 1969
< 1,000–5,300		Cl	Willen 1962
1,800–5,400	5,200	Cl	Chabreck 1960
5,000–6,000		Cl	Ravanko 1972
200–6,900			Husband and Hickman 1985
6,500–7,000		Cl	Kornas et al. 1960
4,033–7,093		SO ₄	Gallup 1978
8,100		Cl	Beter 1957
1,000–8,200	8,200	Cl	Chabreck 1972
1,278–9,904	1,278–4,792	Cl	Thorne-Miller et al. 1983
2,000–10,000		Cl	Eleuterius 1987
3,000–10,000		Cl	Copeland et al. 1974
10,000		Cl	Taylor 1939
> 10,000		Cl	Neely and Davison 1966
	≥10,000	Cl	Heitzman 1978
> 10,000		Cl	Orth 1976
1,300–10,500	6,390	Cl	Saunders and Saunders 1981
1,600–10,500	4,900–10,500	Cl	Jemison and Chabreck 1962
10,500		SO ₄	Brannon 1911
1,400–10,700		Cl	Southwick and Pine 1975
5,690–11,396			Schuler 1987
11,500		Cl	Baldwin 1968
1,000–12,000		HCO ₃ /CO ₃	McCarraher et al. 1961; McCarraher 1962
10,000–12,000		Cl	Klavestad 1957
11,357–12,298		Cl	Percival et al. 1970
8,000–12,320		Cl	Motta 1978
2,500–12,600		Cl	Ungar 1974
9,825–12,900		Cl	Whitman 1976
11,000–13,000		Cl	Harwood 1975
< 13,000		Cl	Carter et al. 1985
7,500–14,000		Cl	Olsen 1945
14,000		SO ₄	Armstrong and Anderson 1966
1,400–14,300		Cl	Gonzalez-Gutierrez 1977 <i>in</i> Verhoeven 1979
9,200–14,400		Cl	Philipp and Brown 1965
6,390–15,975		Cl	Gidden 1965, unpublished data
15,975		Cl	Humm 1956

Table 5. *Continued.*

Salinity or total dissolved solids (mg/L) ^a		Dominant cation(s)	Reference
Range or single observation	Optimum		
< 17,700		Cl	Carl 1937
2,000–18,000		Cl	Maciolek and Brock 1974
2,000–18,000		Cl	Koch and Seeliger 1988
14,000–18,000		Cl	Robarts 1976
17,700–18,600		Cl	Orth et al. 1979
14,900–19,500		Cl	Mahaffy 1987
19,800		Cl	Patriquin and Keddy 1978
> 7,000 –20,000		Cl	Miller 1962
8,000–20,000		Cl	Muus 1967
20,000		Cl	Nilssen 1975
20,000–22,000		Cl	Nixon and Oviatt 1973
5,700–22,200		Cl	Phillips 1960a
2,500–22,500		Cl	Ungar 1968
< 22,500		Cl	Van Vierssen 1982a
5,000–22,800		Cl	Zaouali 1975 <i>in</i> Verhoeven 1979
300–22,900	2,500–12,000	Cl	Larrick and Chabreck 1978
1,520–23,130		Cl	Verhoeven and Van Vierssen 1978b
23,700			Mabbott 1917 (unpublished) <i>in</i> Kantrud 1986
15,000–24,000		Cl	Orth and Moore 1982
10,000–25,000		Cl	Massart 1922
12,000–25,000		Cl	Orth and Moore 1981
15,000–25,000		Cl	Evans et al. 1986
22,600–25,500		Cl	Dawe and White 1986
25,538		Cl	Navarre 1959
13,200–27,700	13,200–14,700	Cl	Tabb et al. 1962
< 28,000		Cl	Martin and Uhler 1939
4,000–28,000		Cl	Jagels and Barnabas 1989
7,000–28,000	22,600	Cl	Zimmerman and Livingston 1979
8,700–28,000		Cl	Wright et al. 1949
15,000–28,000		Cl	Harrison 1982
8,000–29,000		Cl	Wilkinson 1970
9,162–29,560		Cl	Setchell 1924
105–29,750		Cl	Chamberlain 1960
3,000–30,000	3,000–13,000	Cl	Reed 1979
30,000		Cl	Graves 1908
25,000–31,000		Cl	Conover 1961
31,950		Cl	Burk 1962
25,000–32,000		Cl	Pulich 1985
28,000–32,000		Cl	Harlin and Thorne-Miller 1981
< 33,200	<25,000	Cl	Phillips 1960b
2,095–33,324	4,742–22,582	Cl	Joanen and Glasgow 1965
3,000–>35,000		SO ₄	Sloan 1970
< 35,000	10,000	Cl	Neely 1962
< 35,000		Cl	Flores-Verdugo et al. 1988
2,000–35,000		Cl	Zenkevitch 1963
> 35,000		Cl	Osterhout 1906
< 35,200	9,000	Cl	Ferguson Wood 1959
510–35,600		CO ₃ /HCO ₃	McCarraher 1977

Table 5. *Continued.*

Salinity or total dissolved solids (mg/L) ^a		Dominant cation(s)	Reference
Range or single observation	Optimum		
10,500–36,500		Cl	Gore 1965
10,000–38,000		Cl	Swiderek 1982
< 39,900		Cl	Scott et al. 1952
22,000–40,000		Cl	Sullivan 1977
< 40,000		Cl	Anderson 1972
< 45,000		Cl	Simmons 1957
15,000–>45,000		SO ₄	Millar 1976
< 52,500	3,000	Cl	Critcher 1949
3,300–53,000		SO ₄	Hammer et al. 1975
55,300		Cl	Christian 1981
56,000		Cl	Bayly and Williams 1973
2,000–60,000		Cl	Richardson 1980
5,000–60,000		Cl	Edwards 1978
< 60,000		Cl	Conover 1964b
< 60,000		Cl	Thorhaug et al. 1985
16,200–61,400		SO ₄	Hammer and Heseltine 1988
5,500–66,820	5,500–31,000	SO ₄	Tones 1976
< 74,000		Cl	McMillan and Moseley 1967
540–75,694	6,323–18,066	Cl	Verhoeven 1979
457–77,386		SO ₄	Metcalf 1931
90,583		Cl/CO ₃	Wetzel 1964
74,200–95,750		SO ₄	H. A. Kantrud, unpublished data
97,500		Cl	Euliss 1989
< 107,000		Cl	Brock and Shiel 1983
< 110,000		Cl	Wood and Baas Becking 1937
400–118,000		SO ₄	Rawson and Moore 1944
4,800–122,600		Cl	Geddes et al. 1981
92,000–132,000		Cl	Davis and Tomlinson 1974
38,000–156,000		Cl	Davis 1978
12,000–230,000		Cl	Brock 1982a, 1982b
< 260,000		SO ₄	McKay 1934
540–358,000		Cl	Millard and Scott 1953
160,000–390,000		SO ₄	St. John and Courtney 1924 in Verhoeven 1979

^a Conductivity was converted to mg/L with the following multipliers: 0–2 mS \times 0.7; 2–40 mS \times 1.0; >40 mS \times 1.3. Chlorinity (0/00) was converted to mg/L by $\times 1.807 \times 10^3$; sea strength was considered 31,950 mg/L.

of 52 g/L NaCl would not germinate across the temperature range 10–30° C. At the other extreme, wigeongrass can be grown and maintained indefinitely in tap water (Setchell 1924; Mayer and Low 1970; McMillan 1974).

Wigeongrass tolerates salinity increases caused by normal intrusions of ocean water into coastal rivers or bays (Phillips 1960a; Stevenson and Confer 1978). Intrusions of ocean water may actually rejuvenate wigeongrass habitat by mechanically scouring away soft bottom sediments and unwanted vegetative mats

in managed coastal impoundments (Baldwin 1968). Godfrey and Godfrey (1974) opined that wigeongrass habitat in North Carolina is constantly changed by coastal salt marshes that build up and are lost when inlets to the ocean open and close and when storm tides move sand that creates shallow sites for colonization. Eleuterius (1987), however, believed that waters at or near full sea strength, persisting for 2 or more years, inhibited wigeongrass growth in wetlands along the Mississippi coast, and that intrusions of sea water into bays, bayous, and rivers during Hurri-

cane Camille in 1969 further reduced populations. Frequent openings of a man-made spillway later allowed great volumes of fresh water to enter these wetlands, creating brackish conditions and a spectacular growth of wigeongrass that persisted for 17 years.

Nevertheless, rapid salinity fluctuations can be deadly according to Verhoeven (1979), who stated that all *Ruppia* taxa in the Netherlands die when chlorinity rises more than 10 g/L (about 18 g/L salinity) in a few weeks. Early experiments by Graves (1908) showed that wigeongrass leaves died from plasmolysis in 4–5 min when placed in a 30 g/L NaCl solution. Van Vierssen (1982a), in the Netherlands, observed that the best stands of *R. maritima* s.s. occurred where salinity was <22.6 g/L and fluctuated less than 18 g/L in a single year. Richardson (1980) noticed no ill effects on wigeongrass in a New Hampshire tidal marsh when salinities plummeted at least 14 g/L in 24 h. South African wigeongrass survived maximum salinity increases or decreases of 0.2 g/L/h, even though plants died down when salinities were high (Millard and Scott 1953). McKay (1934) found wigeongrass completing its normal drupelet production in a MgSO_4 -dominated lake where salinity increased 44 g/L (16–60 g/L) in the nine weeks after flowering, and he saw little difference in drupelet production when salinity varied about 244 g/L (16–260 g/L) between years.

Wigeongrass occurs in natural waters of pH 6.0 (Joanen and Glasgow 1965) to 10.4 (Verhoeven 1979; Table 6). Pip (1978, 1979, 1984) noticed the affinity of wigeongrass for wetlands of higher pH (7.7–9.4) and the deficiency of the species in the granitic Precambrian Shield region of south-central Canada where waters are usually soft and slightly acidic. Outdoor experiments by Neely (1958, 1962), who was trying to grow wigeongrass by reducing acidity caused by the oxidation of iron polysulfides ("cat clays") on pond bottoms, showed that no plants grew until waters reached pH 5.0. He recommended pH 7.0–8.0 for successful wigeongrass propagation.

Wigeongrass tolerates an extremely wide range of carbonate alkalinity (Table 6). McCarragher (1972, 1977) found wigeongrass in highly saline (>40 g/L) lakes in the Nebraska sandhills; these lakes had total alkalinities up to 34.7 g/L and CO_3 and HCO_3 concentrations of up to 25.4 g/L and 9.3 g/L, respectively. Moyle (1945) believed wigeongrass would not get sufficient nutrients in Minnesota waters containing <150 mg/L total alkalinity. In south-central

Canada, Pip (1978, 1979) also noticed the affinity of wigeongrass for waters with higher than average total alkalinity (86–800 mg/L). However, wetlands with as little as 30 mg/L total alkalinity can support wigeongrass (Chamberlain 1960).

Major nutrients (N, P, K) are readily taken up from the water column by wigeongrass (Setchell 1946; Thursby and Harlin 1984) and extensive beds of the plant have, in at least one case, been created by fertilization with N and P (Davis 1978). However, excessive amounts of the major nutrients can cause phytoplankton blooms and epiphytic growths that can attenuate photosynthetically active radiation (PAR; Twilley et al. 1985). Plants in such environments may suffer early senescence and reduced energy supplies to propagative structures. Plants grown in algae-free culture can prosper under much lower light intensities than when algae are present (Thursby 1984a). All the major nutrients are likely to be found in excessive amounts in highly eutrophic or polluted waters. Although wigeongrass has occasionally been recorded from such waters (Neel et al. 1973; Lein et al. 1974; Nilssen 1975; Zimmerman and Livingston 1979), it seems likely that the poor light conditions usually found in polluted waters would quickly eliminate the plant, considering its high light requirements. Perhaps that is why so little is known about maximum levels of nutrients—or the commonly associated increases in biochemical oxygen demand and chemical oxygen demand—that wigeongrass can tolerate.

For N, the minimum leaf tissue content considered indicative of optimum growth conditions for wigeongrass is 2.5–3.0% (Thursby 1984a). Pip (1978, 1979) showed the affinity of wigeongrass for waters with higher than average values of N (0.9–6.8 mg/L) in interior Canada. I could find no records for the plant in waters with less than 0.6 mg/L total N (Table 6). Attempts by Harlin and Thorne-Miller (1981) to measure the effects of NO_3 and NH_3 additions on wigeongrass in situ were thwarted by growths of green algae.

Phosphorus concentrations of at least 0.3% in wigeongrass leaf tissue indicate optimum growth conditions (Thursby 1984a). Conover (1961) found densest stands of wigeongrass in a coastal Rhode Island wetland where bottom waters were rich in P. Harlin and Thorne-Miller (1981) found, also at a Rhode Island site, that P fertilization in situ stimulated wigeongrass biomass and resulted in longer leaves. Holmes (1972) suggested that P limits wigeongrass growth even in wetlands where 15 $\mu\text{g/L}$ are available during the nongrowing season. Robarts (1976)

Table 6. *Chemical content of natural waters inhabited by wigeongrass (Ruppia maritima).*

Characteristic	Unit of measure	Range or single observation (reference ^a)
pH and alkalinity system		
pH		6.0 – 10.4 (1;2)
Total alkalinity	g/L CaCO ₃	0.030 – 34.7 (3;4)
HCO ₃ alkalinity	g/L CaCO ₃	0.032 – 9.3 (5;4)
CO ₃ alkalinity	g/L CaCO ₃	0.0 – 25.4 (6;4)
CO ₂	mg/L	0.0 – 12.0 (3)
Nutrient system		
Total N	mg/L	0.6 – 14.0 (7;8)
NO ₂ -N	mg/L	0.0 – 0.17 (6)
NO ₃ -N	mg/L	0.0 – 7.1 (8;9)
NH ₃ -N	mg/L	0.01 – 2.6 (10;6)
P dissolved	mg/L	0.0 – 1,200 (11;8)
PO ₄ -P	mg/L	0.06 – 4.94 (10;12)
K	mg/L	6.0 – 2,300 (13;8)
Other elements and compounds		
Al	μg/L	10 – 100 (8)
As	μg/L	48 – 250 (8)
Ba	μg/L	100 – 400 (8)
B	mg/L	2.2 – 17.0 (8)
Ca	mg/L	11 – 1,620 (14;5)
Cd	μg/L	0.0 – 2.0 (8)
Cl	g/L	0.0 – 70.6 (15;5)
Co	μg/L	0.0 – 2.0 (8)
Cr	μg/L	0.0 – 2.0 (8)
Cu	μg/L	0.0 – 3.0 (8)
Fe	μg/L	39 – 450 (12;8)
Fl	mg/L	0.1 – 9.5 (8;16)
Hg	μg/L	0.1 – 0.5 (8)
Li	mg/L	4.0 – 13.0 (8)
Mg	g/L	0.01 – 54.0 (13;17)
Mn	μg/L	100 – 620 (8;12)
Mo	μg/L	1.0 – 10.0 (8)
Na	g/L	0.018 – 49.0 (13;8)
Ni	μg/L	0.0 – 12.0 (8)
Pb	μg/L	3.0 – 13.0 (8)
Se	μg/L	1.0 (8)
SiO ₂	mg/L	7.9 – 12.0 (8)
SO ₄	g/L	0.0 – 244.0 (3;17)
Sr	μg/L	120 – 570 (8)
V	μg/L	63 – 280 (8)
Zn	μg/L	60 – 230 (8)

^a Reference: 1—Joanen and Glasgow 1965; 2—Verhoeven 1979; 3—Chamberlain 1960; 4—McCarraher 1977; 5—Geddes et al. 1981; 6—Neel et al. 1973; 7—Davis 1978; 8—U.S. Geol. Surv., unpubl. data., Eastern Stump Lake, Nelson County, North Dakota, May–October 1976–1979; 9—Gallup 1978; 10—Orth and Moore 1982; 11—Robarts 1976; 12—Van Vierssen 1982b; 13—Haag and Noton 1981b; 14—U.S. Fish Wildl. Serv., unpubl. data., “Wigeon Lake”, Kidder County, North Dakota, September 1965; 15—Pip 1979; 16—Navarre 1959; 17—Anderson 1958 in Ungar 1974.

saw $\text{PO}_4\text{-P}$ levels fall to zero in wigeongrass-inhabited waters when diatom populations were high, even though up to $18\text{ }\mu\text{g/L}$ was available at other times. Total P fell to 0.1 mg/L by August in a Minnesota lake supporting wigeongrass (Neel et al. 1973). Phosphorus seemed more important than N in controlling the growth of *Ruppia megacarpa* in an Australian estuary (Lukatelich et al. 1987).

Known effects of water-column K on wigeongrass are limited to the findings of Setchell (1946), who found that plants could be cultured for years in tapwater if KNO_3 were added.

Table 6 shows the ranges in concentration of many other elements in natural waters inhabited by wigeongrass. Much other information on the tolerance of wigeongrass for these and other uncommon elements is available from irrigation drainwater evaporation ponds in California where high concentrations of Se and B have accumulated (Saiki and Lowe 1987; Schuler 1987; Schroeder et al. 1988).

Little work has been done on the effects of non-nutrients or micronutrients on wigeongrass. Setchell (1946) found that wigeongrass could be cultured without sediment in distilled water if MgSO_4 was added. Moyle (1945) established a lower limit of 50 mg/L SO_4 for Minnesota wigeongrass, but the plant was found in Florida waters where no sulfates were detected (Chamberlain 1960). Van Vierssen (1982b) indicated that wigeongrass mostly grew in waters where molar Ca/Mg and K/Mg ratios were low.

In summary, *R. maritima* s.l., despite its otherwise rather narrow ecological niche, occupies wetlands having a greater range of salinity than is tolerated by any other submersed angiosperm. Optimum salinity for wigeongrass growth in Cl-dominated wetlands is about $5\text{--}20\text{ g/L}$, but somewhat lower salinities earlier in the growing season may enhance rapid germination and drupelet production. Salinities for best growth in inland, SO_4 -dominated waters are about twice as high as in Cl-dominated waters. The effects of salinity fluctuations on wigeongrass are unclear. Wigeongrass does poorly in fresh, soft, or even slightly acidic waters. Nutrients are readily absorbed from the water column and can stimulate growth, but in eutrophic waters growth is often severely limited by phytoplankton and epiphytes.

Temperature

Growth of wigeongrass may be more strongly influenced by water temperature than other impor-

tant environmental variables. For example, in a temperate estuary, time of maximum wigeongrass biomass coincided with period of peak summer temperature rather than with period of maximum insolation (Conover 1958), and growth of the plant in Texas lagoons was positively correlated with cool spring temperatures rather than with low salinities (Pulich 1985). Shallow water forms of wigeongrass must be resistant to cold as well as drought (Verhoeven 1980a).

Water temperature, of course, affects phenology. In western Europe, Verhoeven (1979) found that drupelet germination and rhizome budding began after winter during the first 10 days when mean daily minima and maxima water temperatures exceeded 10° and 15°C , respectively, and that reproductive processes began only in 10-day periods when temperatures attained $15\text{--}19^\circ\text{C}$. In Chesapeake Bay, wigeongrass tends to form monotypic stands in shallow intertidal and shallow subtidal areas where summer water temperatures and transparencies are high; peak biomass occurs later in the growing season after waters cool (Wetzel et al. 1981). In Rhode Island, wigeongrass actively grows from late April to late October; growth lags attrition in fall when water temperatures fall to 12°C (Conover 1964a). In North Carolina, production ceases in October when water temperatures fall below 18°C (Reed 1979). In the southern United States, midsummer die-offs of wigeongrass are common in impoundments and likely occur because of direct and indirect effects of high summer temperatures and increased salinity (Swiderek 1982). Prevost (1987) stressed the need for water circulation during warm summer to early fall in these wetlands to help flush out cloaking filamentous algae. It is likely that growth periods of these algae are associated with high water temperatures. Richardson (1980) suggested that flowering, fruiting, and drupelet production are lengthened by temperature stratification caused by dense algal mats and vegetation.

The distribution of wigeongrass also can be affected by temperature. Anderson (1969) saw *Potamogeton perfoliatus* (thorowort pondweed) replace wigeongrass near an area of thermal effluent discharge where water temperatures sometimes reached 35°C . He suspected that this temperature allowed survival, but not growth, of wigeongrass rhizomes.

In North America, the overall water temperature range at which annual-like wigeongrass completes its life cycle is about $10\text{--}33^\circ\text{C}$. Drupelets germinate

at about 10–20° C (optimum 15–20° C; Setchell 1924; Richardson 1980). Optimum germination temperatures for drupelets from *Ruppia* taxa from other parts of the world can differ by as much as 20° C (Seeliger et al. 1984; Van Vierssen et al. 1984; Koch and Seeliger 1988). In Italy, Ortu (1969) found that the latency or dormant period of wigeongrass drupelets decreased with increased temperature but that low temperatures probably increased the germination rate of those held at relatively low salinities. Koch and Seeliger (1988) showed that drying of wigeongrass drupelets collected from an ephemeral habitat in Brazil increased germination, but high temperatures and low salinities induced germination in drupelets collected from a nearby, more stable habitat.

Seedlings develop at about 15–25° C (optimum 15–20° C; Setchell 1924; Joanen 1964; Richardson 1980). Vegetation grows at 12–33° C (Conover 1964a; Joanen 1964; Nixon and Oviatt 1973; Orth et al. 1979; Richardson 1980; Harlin and Thorne-Miller 1981). Optimum growth temperatures in Rhode Island are 12–18° C, whereas those in North Carolina are 18–22° C (Reed 1979). Phillips (1960a) found wigeongrass abundant in a Florida river when temperatures ranged from 18 to 29° C.

Flowering, pollination, and drupelet production proceed at water temperatures of about 18–32° C (Setchell 1924; Phillips 1960a; Conover 1964a; Joanen 1964; Richardson 1980). Setchell (1924) reported that optimum reproductive temperatures are 20–25° C and that anthesis is slow and eventually ceases after prolonged periods above 25° C.

It is likely that water temperatures exceeding 30° C are harmful or lethal to the development of wigeongrass in most north temperate wetlands (Vicars 1976; Verhoeven 1979). Nevertheless, Edwards (1978) measured water temperatures up to 36° C in a Mexican lagoon dominated by wigeongrass. A perennial wigeongrass in Florida withstands 39.4° C, but flowering and growth are inhibited in temperatures >30° C (Phillips 1960a). Laboratory tests of Anderson (1966) showed that wigeongrass cells died when exposed to 40° C for 30 min and all cortical aerenchyma perished in 15 min at 45° C.

Water Movement

Wigeongrass prospers in still or protected waters and sometimes in rather strong currents but not in areas with excessive turbulence (Transeau 1913; Johnson and York 1915; McAtee 1939; Day 1952; Wood

1959; Orth et al. 1979; Verhoeven 1979). Wave action in small wetlands restricted wigeongrass to areas deeper than 10 cm (Davis 1978). In large open wetlands, wave action limits the growth of wigeongrass either through mechanical injury or—in wetlands with easily-suspendible bottom sediments or large amounts of vegetative debris—through increases in turbidity (Smith 1951; Joanen 1964; Joanen and Glasgow 1965; Swiderek 1982). Vicars (1976) suggested reduced wave action as one of the factors causing relatively stable wigeongrass biomass during a nearly twofold increase in plant density in a North Carolina estuary. Wave action injures surface branches of wigeongrass, leaving broken tips incapable of survival (McCann 1945). Sometimes only sterile plants are found at exposed sites (Luther 1951 in Verhoeven 1979). Wigeongrass is rarely seen along wave-exposed shorelines of Chesapeake Bay unless associated with *Zostera marina*; monospecific beds of wigeongrass are mostly found in areas protected from wave action (Orth and Moore 1988). Algal felts or mulch from previous years growth helps protect wigeongrass seedlings from wave damage or associated turbidity (Gore 1965; Richardson 1980).

Wind-induced turbidity can limit wigeongrass productivity (Harwood 1975) and sometimes be more important than planktonic algae in that respect (Conover 1964a). Williams (1979) and Gerbeaux and Ward (1986) attributed the lack of regeneration of *Ruppia* for many years after a storm to a combination of the removal of fine sediments and increased phytoplankton blooms. The latter probably was the main cause, however, considering the high light requirements of *Ruppia* and that its habitat may be rejuvenated by occasional removal of soft sediments (Baldwin 1968).

Because of its shallow and rather weak root system, wigeongrass usually grows better in lagoons and bays where current flow is less than in channels, main basins, and tidal rivers (Ferguson-Wood 1959; Reed 1979; Congdon and McComb 1981). Kerwin et al. (1976) speculated that the flushing action of river water after tropical storm Agnes could have been a factor in decreased wigeongrass in Chesapeake Bay.

In some cases, wigeongrass can be extremely robust in areas of considerable current flow. Saunders and Saunders (1981) found some of the most luxuriant and productive stands of wigeongrass in Mexican lagoons where currents swept flocculent silts out to sea. They also suggested that habitat for wigeongrass and other choice submersed plants eaten by

wintering waterfowl improves in subtropical lagoons when hurricanes scour away soft silts and flush out beds of floating pest plants. Conover and Gough (1966) and Richardson (1980) attributed the robustness of wigeongrass in areas of current flow to a better supply of nutrients and dissolved gases to leaf surfaces and the near absence of epiphytes. Wigeongrass beds fertilized in situ with P grow well in currents up to 4 cm/s (Harlin and Thorne-Miller 1981). Davis (1978) saw wigeongrass flourish and produce drupelets in areas with high rates of water flow but did not verify sexual reproduction.

Philip (1936) considered wigeongrass to have many features that adapt it to fluctuating water levels. The species occurs, sometimes in great abundance, in bays, lagoons, or channels with tides up to 1 m (Scott et al. 1952; Nixon and Oviatt 1973; Larrick and Chabreck 1978; Getsinger et al. 1982). It is common in—or sometimes almost restricted to—intertidal zones exposed to air up to 4 h daily (Johnson and York 1915). Keddy (1987) found wigeongrass at sites exposed up to 6.96 h at each low tide. Where exposure times are greater, such as in drained pannes or desiccated inland wetlands, wigeongrass quickly disappears (Bourn and Cottam 1950; Chapman 1960; Bolen 1964; Congdon and McComb 1979). In British Columbia, Bigley and Harrison (1983) observed that exposure of wigeongrass beds to air in tidal areas results in fewer shoots, less drupelet production, and earlier flowering. Nevertheless, length of the life cycle remains the same in plants found lower in the intertidal zone. McCann (1945) believed that wigeongrass would die quickly if exposed to direct sunlight.

Stable water provides good growing conditions for wigeongrass in managed wetlands; however, water circulation and incremental water-level increases may be required (Singleton 1951; Beter 1957; Prevost 1987). The plant withstands prescribed drawdowns for wildlife management purposes, but excessive or irregular water level fluctuations that expose bottom soils for long durations eliminate existing stands or cause great difficulty in establishing new stands (Joanen 1964; Joanen and Glasgow 1965). When tidal and seasonal water inundation was restored to Florida impoundments, wigeongrass was replaced by annual and perennial glassworts (*Salicornia* spp.) and black mangrove (*Avicennia germinans*; Gilmore 1987).

Water level fluctuations can affect wigeongrass indirectly by influencing water chemistry. Kimble and Ensminger (1959) reported that abnormal high tides during a hurricane probably distributed wigeongrass

into interior marshes where the influx of saline water and slow runoff created favorable conditions for growth. Conversely, water level increases between growing seasons in subsaline prairie wetlands often result in the replacement of wigeongrass by luxuriant growths of the less salinity-tolerant sago pondweed and muskgrass (H. A. Kantrud, personal observation).

I found no information on the effects of ice action on wigeongrass. I noted little change in the distribution of wigeongrass in highly saline North Dakota wetlands as long as the area inundated remained similar between growing seasons. These wetlands freeze to the bottom every winter, and their wigeongrass populations behave as annuals, producing many drupelets. Although there is no evidence, wind-driven ice or "ice lift" of bottom sediments (Martin and Uhler 1939) possibly could be a factor in the distribution of wigeongrass in deeper waters where the plant likely would grow as a perennial and depend on overwintering rhizomes for reproduction.

Bottom Substrate

Texture

The influence of light, temperature, exposure, and salinity on wigeongrass was so large that Luther (1951 in Verhoeven 1979) and Verhoeven (1979) considered substrate preferences to be of secondary importance. Nevertheless, it is probable that long diffusion distances and low rates of diffusion and exchange of nutrients are important factors limiting growth of submersed macrophytes in coarse bottom substrates (Barko and Smart 1986).

McAtee (1939) stated that wigeongrass grew in bottom sediments ranging in texture from sands to mucks. In fact, wigeongrass can easily be grown without sediment (Setchell 1924; Seeliger et al. 1984; Thursby 1984a; Thursby and Harlin 1984), and plants can lose all roots in highly reduced organic soils and grow on the water surface (Conover 1964a). Despite these observations, I present information here that may be useful to wetland managers regarding possible interactions between wigeongrass and substrate.

Bottom substrate texture is related to physical and chemical conditions, so it is difficult to prove that texture per se is important in the distribution of submersed hydrophytes. For example, Higginson (1965) related the distribution of *Ruppia spiralis*, *Halophila ovalis*, and *Zostera capricorni* in some nutrient-rich, coastal Australian lakes to sediment nutri-

ents; organic matter content, minerals, and texture; and water depth. He found the presence of pure *Ruppia* stands closely related to areas of greater water depth, higher sediment clay and organic matter content, and lower sediment sand content. He concluded that (1) concentrations of nearly all nutrients and minerals were highest in sediments of greatest clay content, but there was no evidence that this increased fertility was caused by chemical rather than physical characters; (2) the zonation of the plants was the result of differences in sediment conditions; and (3) an interaction of depth and sediment type adequately explained the distribution of the plants.

The effects of sediment texture may interact with salinity. In Alberta, Canada, Husband and Hickman (1989) found that frequency of occurrence of a perennial-like *Ruppia* depended on sediment texture in two mixosaline lakes but not in a freshwater lake, where the plant was found primarily on coarse-textured substrates. When in freshwater, the absence of the plant from fine-textured sediments was not correlated with the abundance of other macrophytes. Local abundance in relation to sediment texture was similar among lakes. Abundance was not significantly correlated with lake salinity, except on sandy sites. They suggested that the effects of salinity on the colonization of new sites, rather than the performance of the plant within sites, was important in determining the distributional limits of the plant.

Table 4 lists the predominant substrate texture for many stands of *Ruppia maritima* s.l. worldwide. Nearly all wigeongrass that grew in waters deeper than 2.0 m occurred on sand or shell bottoms, whereas all records for clay and silt bottoms were in waters <1.5 m deep. This is probably attributable to differences in light attenuation of waters overlying sediments of varying susceptibility to resuspension by wave action.

Martin and Uhler (1939) considered wigeongrass to be more tolerant of firm sand than any other submersed plant eaten by waterfowl. *Ruppia* often grows well on sand in thalassic nearshore flats, bays, fjords, and estuaries and in the rivers that empty into them (Olsen 1945; Conover 1958; Kornas et al. 1960; Strawn 1961; Philipp and Brown 1965; Muus 1967; Tenore 1972; Copeland et al. 1974; Van Vierssen 1982a). Coastal wigeongrass populations studied by J. L. Sincock (1965, unpublished data) grew best on sand, followed by shell, loam, and silt; plants were less frequent on clay, muck, and peat in an area where turbidity limited growth. Shell or muddy sand support abundant wigeongrass growth

in a spring-fed coastal river in Florida (Phillips 1960a). Pulich (1985) indicated that wigeongrass adapts to nutrient-poor substrates containing little organic matter but up to 72–98% sand and shell. However, Thorne-Miller et al. (1983) found better growth in fine sands containing substantial organic matter. Wigeongrass also commonly occurs on sandy bottoms in athalassic waters (Moyle 1945; Neel et al. 1973; McCarraher 1977).

Wigeongrass growth diminishes when natural sandy-organic sediments are replaced by washed sand, even when plants are submersed in the natural waters of their origin (Moyle 1945). In culture, *Ruppia maritima* s.s. achieves exponential growth earlier on sand than on mud even though plants growing in mud are nearly twice as heavy after 4 months of growth (Verhoeven 1979).

Silt bottoms in coastal lagoons and estuaries support wigeongrass (Koch et al. 1974; Dawe and White 1986). Silt (and marl) bottoms in mixosaline Alberta wetlands are generally high in frequency and abundance of a perennial *Ruppia* (Husband and Hickman 1989). Olsen (1945) and Gore (1965) opined that soft bottoms would not easily support wigeongrass because of the susceptibility of seedlings to wave action. Indeed, in a Massachusetts estuary, wigeongrass was absent on soft flocculated silts but present on nearby sands (Conover 1958). Similarly, many years of observations on wigeongrass in large lagoons in Mexico suggested that soft flocculated silts were inhospitable to the plant, whereas firm bottoms of a wide variety of other textural types supported luxurious stands (Saunders and Saunders 1981).

Clay bottoms, especially in sheltered areas, are favorable for wigeongrass (Joanen and Glasgow 1965; Pehrsson 1984). Swiderek (1982) found much higher wigeongrass production in South Carolina ponds with firm clay substrates than in ponds with soft bottoms subject to increased sedimentation and wind-induced turbidity. During the hot summer months, wigeongrass also persisted longer in the clay-bottomed ponds, and Swiderek recommended reserving these ponds strictly for propagation of wigeongrass rather than other waterfowl foods. Jensen (1940) believed Utah wigeongrass could not compete with *Potamogeton pectinatus* except on heavy clays with little organic content. Craner (1964) also found that Utah wigeongrass thrived on heavy clays but survived poorly when coexisting with *P. pectinatus* in silts and clay loams. Verhoeven (1979) associated western European wigeongrass with clay bottoms high in organic content (3–10% of dry weight). Density of wigeongrass

was also highest on organic clays in Finland and clay-bottomed wetlands in the Netherlands (Van Vierssen 1982a). In Utah, organic clay bottoms and upland clay soils, when flooded artificially, quickly produced a fair crop of wigeongrass that followed an initial growth of *Chara* (Nelson 1954). In Australia, *R. spiralis* is monodominant only on bottoms high in clay content (42.3%); where amounts are less, mixed stands or other plants occur (Higginson 1965).

Wigeongrass is moderately productive on loam bottoms according to J. L. Sincock (1965, unpublished data). A higher standing crop of *Ruppia maritima* s.s. grew on mud than on sand; Verhoeven (1979) attributed this to the higher nutrient content of the former substrate. *Ruppia* cultured by McRoy and McMillan (1977) showed better survival on fine sandy loam than on river sand and plants flowered only on the loam. I found no other specific references to loam, but "muds"—especially those of a sandy or silty nature—were often mentioned as wigeongrass habitat (Klavestad 1957; Tabb et al. 1962; Eleuterius 1971; Getsinger et al. 1982).

Bottoms of fibric (peats), hemic (mucks), or sapric (spropels or gyttja) organic materials often support wigeongrass (McAtee 1939; Stieglitz 1966; Verhoeven 1979; G. S. Gidden, 1965, unpublished data), and the plant sometimes is the most common submersed macrophyte on these bottoms (Spiller and Chabreck 1976; Van Vierssen 1982a). Some of the highest biomasses of wigeongrass occur on sediments high in organic content (up to 10 kg/m² dry weight or 57% organic matter in a 3–5-cm core; Higginson 1965; Nixon and Oviatt 1973; Edwards 1978). In saline Saskatchewan lakes, the best beds of *Ruppia* occur where clay bottoms are covered by a layer of organic matter (Tones 1976). Heitzman (1978) noted luxuriant wigeongrass growth on firm organic bottoms, as long as they remained free of silt and detritus. However, Mahaffy (1987) saw better wigeongrass growth in sediments that contained <3% organic matter.

In summary, with the possible exception of rubble or bedrock, wigeongrass can grow on all common bottom substrates found in nature. Flocculated silts probably are the least favorable bottom substrate for wigeongrass growth. Under highly reducing conditions, plants lose their root system but can sometimes live suspended in the water column in sheltered wetlands. Plants will be found in deeper water and will be less subject to wave damage where bottoms are firm or coarse-textured and less subject to particle resuspension. However, plants growing in pro-

tected areas where bottoms are usually fine-textured and rich in nutrients and organic matter will produce greater biomass.

Sedimentation and Disturbance

After erosion carries particles of upland soils into wetlands, the newly deposited sediments move by wave action to central deeper areas or are trapped by vegetation in sheltered peripheral areas. No mechanism may exist to move sediments in extremely protected areas. Colloidal particles tend to flocculate with increasing salinity, thereby increasing water clarity. It is in riverine habitats and shallow areas subject to long wind fetches that submersed macrophytes are most likely to be damaged by sedimentation (Vicars 1976; Bellrose et al. 1979). Plants with highly dissected leaves can easily be crushed or coated by sediment and are at a disadvantage to linear-leaved species, such as wigeongrass (Schiemer and Prosser 1976; Vander Zouwen 1982). Millard and Scott (1953) saw wigeongrass prosper in portions of a South African estuary that experienced nearly constant inflows of fine silts and colloidal clays whenever surface water was present, but they did not measure silt deposition rates.

There is some evidence—but no experimental data—that wigeongrass is quite tolerant of disturbance. Chapman (1960) remarked on luxuriant beds of wigeongrass in Iraqi waters much disturbed by water buffalo (*Bubalis bubalis*). Breuer (1961 in Cornelius 1975) mentioned that the plant occurs around emergent deposits of dredge spoils in the Laguna Madre, Texas. Ward and Armstrong (1980) predicted that turbidity caused by dredging a Texas lagoon would only temporarily lower wigeongrass productivity and might, after plant recovery, increase it—but no subsequent surveys were conducted. In Nebraska, wigeongrass has been noted in excavated, flooded sandpits (Larson and Martin 1972).

Chemistry

Wigeongrass propagules occur in chloride-dominated bottom substrates that contain up to 7.2% salts, although vegetation frequently dies back at lower concentrations (Flowers 1934; Jensen 1940; Millard and Scott 1953; Bolen 1964; Gore 1965; Flowers and Evans 1966; Ungar 1968; Percival et al. 1970). Wigeongrass grows in coastal Louisiana sediments with 0.89–2.99% salinity; maximum growth occurs at 0.89–1.72% (Joanen 1964; Joanen and Glasgow 1965). It was suspected that growth by rhizomes was

responsible for maintenance of large stands where sediments contained >1.12% salts because drupelets germinated poorly.

Sediments that support wigeongrass vary in pH from 3.1 to 8.8 (Table 7). Wigeongrass prospers at the lower end of this range if water-column pH does not fall below 6.5 (Wilkinson 1970). Nevertheless, acidification of bottom substrates, a result of oxidation of iron polysulfides, is a serious problem for managers of wigeongrass impoundments in the southern United States (Neely 1958, 1962; Swiderek 1982).

Better growths of wigeongrass can occur in sediments where concentrations of inorganic N and P are highest (Conover 1958). In infertile waters, sediments are an important source of nutrients for wigeongrass (Husband and Hickman 1985). In eutrophic waters, wigeongrass probably does not depend on sediments for nutrients, even though roots are active assimilation sites and root development is a direct function of the chemical environment where the plants occur (Conover 1964a; Conover and Gough 1966).

Table 7. *Chemical characteristics of bottom sediments used by wigeongrass (Ruppia maritima).*^a

Characteristic	Unit of measure	Range or single observation (reference ^b)
pH		3.1 – 8.8 (1;2)
Nutrient system		
Total N	mg/g	1.8 – 4.7 (3)
NO ³ -N	mg/L	0.022 – 1.1 (4)
Total P	mg/kg	270 – 320 (3)
Soluble P	mg/kg	13.2 – 20.5 (3)
Soluble P	mg/L	7.0 – 37.1 (5;6)
PO ⁴ -P	µg/L	0.03 – 300 (4)
K	mg/g	0.03 – 0.51 (7)
K	mg/L	32 – 611 (6)
Other elements		
Al	mg/L	11.2 – 845.7 (6)
Ba	mg/L	0.02 – 1.23 (6)
B	mg/L	1.95 – 23.71 (6)
C	mg/g	22 – 52 (3)
Ca	g/L	0.09 – 3.3 (6;5)
Cd	mg/L	0.0 – 0.24 (6)
Co	mg/L	0.32 – 4.73 (6)
Cr	mg/L	0.09 – 0.89 (6)
Cu	mg/L	0.06 – 0.89 (6)
Fe	mg/L	2.25 – 533.7 (6)
Mg	mg/g	0.07 – 0.51 (7)
Mg	g/L	0.1 – 2.6 (1;6)
Mn	mg/L	5.2 – 21.0 (6)
Mo	mg/L	2.3 – 4.4 (6)
Na	mg/g	0.4 – 4.8 (7)
Na	g/L	0.2 – 3.5 (6)
Ni	mg/L	1.93 – 2.11 (6)
Pb	mg/L	0.06 – 3.45 (6)
Si	mg/L	19.5 – 66.3 (6)
Sr	mg/L	7.2 – 50.3 (6)
Zn	mg/L	0.0 – 15.8 (6)

^a Wet weight measurements from extracted waters; other measurements on a dry weight basis.

^b Reference: 1—Wilkinson 1970; 2—Flowers 1934; Flowers and Evans 1966; 3—Neel et al. 1973; 4—Conover and Gough 1966; 5—Percival et al. 1970; 6—Swiderek 1982; 7—Verhoeven 1979.

Nitrogen concentrations as high as 4.7 mg/g have been found in sediments supporting wigeongrass (Neel et al. 1973; Table 7). Joanen and Glasgow (1965) measured lower levels of available sediment P in wetlands that yielded larger amounts of wigeongrass and, within individual wetlands, lower amounts of P inside wigeongrass stands than outside them. This suggested active uptake of this essential element by wigeongrass roots. Levels of sediment K in stands of wigeongrass did not change during 10 months of this study. Verhoeven (1979) found no relation between K concentrations of three *Ruppia* taxa and the amount of K in either the sediment or water column.

Sediment Mg and Ca showed little or no change during 10 months in the wigeongrass ponds studied by Joanen (1964) and Joanen and Glasgow (1965). Verhoeven (1979) found that, although the Mg content of *Ruppia* plants show no relation to environmental Mg, the Ca and Na content of the plants relate to that of the sediments and water column. Higginson (1965) found *R. spiralis* associated with greater amounts of sediment N, K, Mg, Fe, and organic matter, but with lesser amounts of Ca.

It is likely that *Ruppia* plants favor aerobic sediments with low levels of sulfides and free H_2S (Conover and Gough 1966; Baldwin 1968; Lipkin 1977; Davis 1978; Pulich 1989). Nevertheless, wigeongrass frequently occupies reduced sediments where leaves supply oxygen to the roots. Plants without rhizome systems can grow suspended in ooze in extremely reduced sediments (Conover and Gough 1966). Such beds must occur only in very sheltered locations.

Concentrations of micronutrients and trace elements found in natural sediments supporting wigeongrass are shown in Table 7. Similar data for these and many other less common elements are available for irrigation drainwater evaporation ponds in California (Severson et al. 1987; Schroeder et al. 1988).

Biotic Communities and Associated Limiting Factors

Macrophyte

Wigeongrass is a main source of primary production in some subtropical lagoons (Edwards 1978)

and often totally dominates certain portions of estuaries where proper conditions of depth, salinity, and shelter exist (Reed 1979). Other submersed macrophytes often replace wigeongrass quickly when environmental conditions change. Wallentinus (1979) believed that the limited competitive ability of wigeongrass, not its reaction to salinity, nutrient loadings, or other habitat characteristics, is one important reason the plant is restricted to certain shallow habitats in thalassic waters. Hammer and Heseltine (1988) thought that lack of competition allows wigeongrass to dominate more saline habitats. Husband and Hickman (1985) postulated that *Ruppia* may require saline water and not merely be at a competitive disadvantage in fresh water. However, recent research does not support the theory of salt enhancement of metabolic activity for submersed vascular plants (Jagels and Barnabas 1989).

In any case, wigeongrass commonly occurs in mixed stands at both ends of the salinity gradient and coexists well with some other submersed angiosperms. For example, Harrison (1982) found little effect of wigeongrass on growth of *Zostera japonica*, and Keddy (1987) observed that the presence or absence of wigeongrass did not affect the number of spathes produced by the annual form of *Z. marina*.

Wigeongrass also intersperses with small-to-medium-sized emergents, such as *Cladium* (sawgrass), *Eleocharis* (spikerush), or *Juncus* (rush; Joanen 1964; Joanen and Glasgow 1965; Baldwin 1968), or taller forms, such as *Scirpus americanus* (American bulrush), *S. maritimus* (alkali bulrush), or *Typha domingensis* (southern cattail; Chapman 1960; Jefferson 1974; Zedler and Nordby 1986). Indeed, a more diverse flora occurs in coastal wigeongrass impoundments than in adjacent tidal wetlands (Kelley and Porcher 1986). Emergent, floating, and submersed plants found with *Ruppia* sp. in some New Zealand lakes are listed by Tanner et al. (1986). Britton and Podlejski (1981) listed many emergents associated with wigeongrass in the French Camargue.

A great variety of submersed macrophytes is associated with wigeongrass around the world (Table 8). Several other submersed macrophytes not shown in this table (such as the charophytes *Nitella* and *Tolypella*) sometimes associate with wigeongrass (Kornas et al. 1960; Verhoeven 1980a; Getsinger et al. 1982).

Although the information in Table 8 does not reflect a random sample of wigeongrass habitat, it is probable that the most important potential competitors of wigeongrass are *Potamogeton pectinatus*, *Chara*

spp., and *Zannichellia* spp. (poolmats). These taxa also have wide global distribution. That these taxa are generally euryhaline perhaps supports the exclusion of wigeongrass from the true seagrasses, even though the plant commonly grows with at least two seagrasses, *Zostera* spp. and *Halodule wrightii*.

The distribution of the plants listed in Table 8 shows the wide environmental tolerance of wigeongrass. The plant occurs in fresh to saline coastal and interior waters on several continents. On the basis of species preference for fresh or saline wetlands, the wigeongrass occurrences on the right side of Table 8 probably are in saline and quite turbid waters, whereas those on the left are probably clear and fresh and neutral, or only slightly acidic, wetlands, where wigeongrass is likely a weak competitor among the specialist taxa (Pip 1984).

Verhoeven (1980a) believed that intra- and inter-specific competition for space, light, and nutrients greatly alters the survival of all *Ruppia* taxa in thalassic waters. He stated that the ultimate success of these plants is determined primarily by the number of hibernating propagules that began spring growth, the pattern and rate of growth under prevailing conditions, and the ability to survive and adapt to temporarily unfavorable conditions.

Environmental changes during the growing season are often mentioned as factors that allow wigeongrass to coexist with other submersed plants. Pulich (1985) suggested that, even when behaving as a perennial, Texas wigeongrass would be replaced by the seagrass *H. wrightii* under favorable growth conditions because of the latter plant's greater below-ground biomass. He later showed how organic C and N gradients, combined with seasonal temperature cycles, could control competitive interaction between the two species by controlling sulfate reduction activity in the sediments (Pulich 1989). Wigeongrass prospered in the cool spring and fall months when sediments were low in free H_2S , whereas *H. wrightii* grew during the warm summer months when sediments often contained free H_2S and high levels of NH_4 . These two species also coexist in a Florida bay, with *H. wrightii* most prominent during winter and wigeongrass most prominent when salinities fall to 13.2–14.7 g/L during July (Tabb et al. 1962). When salinities decrease to 5–10 g/L, *Chara* nearly eliminates the wigeongrass. Although there is some overlap, wigeongrass and *Zannichellia palustris* (horned poolmat) separate temporally in some North Carolina creeks (Davis et al. 1985). There, the latter grows better in late winter and spring, while wigeongrass

flourishes in summer and fall. Newly flooded ditches in Utah had an initial flush of *Z. palustris* and *Chara* sp. in June, but these were replaced by wigeongrass and *Potamogeton pectinatus* by September (Kadlec and Smith 1984).

In North Carolina impoundments, wigeongrass shows poor growth when mixed with *P. pectinatus* if salinities fall below 10 g/L (Heitzman 1978). Reed (1979) saw *P. perfoliatus* replace wigeongrass in a North Carolina estuary as water temperatures rise during midspring and summer. Jensen (1940) believed wigeongrass could not replace *P. pectinatus* in bottom substrates of insufficient clay and organic matter.

Replacement of *Ruppia*-dominated communities by emergent communities is uncommon in highly saline habitats—wigeongrass productivity is usually low there, and organic matter accumulations are insufficient to noticeably raise bottom elevations (Verhoeven 1980a). Nevertheless, Davis (1978) noted that wigeongrass trapped silt that aided colonization of other plants in silty-bottomed, hypersaline solar evaporation ponds. In brackish waters with sandy bottoms, Dahlbeck (1945) and Gillner (1960; both in Chapman 1974) noted that a community dominated by *Zostera nana*, *Ruppia maritima*, and *R. spiralis* later became dominated by *Eleocharis parvula* (dwarf spikerush). Baldwin (1968) recommends protecting the natural *Cladium-Juncus* community around wigeongrass impoundments that are managed for waterfowl in the southeastern United States to prevent invasion by *Typha domingensis*. Stands of wigeongrass along the Oregon coast can be replaced by *Scirpus americanus* where soils are sandy and *S. maritimus* where soils are silty (Jefferson 1974). Probably because of shading, *Juncus roemerianus* (needle rush) and other emergents can lower wigeongrass production more than 50% in coastal North Carolina impoundments. Prevost (1987) listed *Juncus roemerianus* and *Spartina alterniflora* (smooth cordgrass) as major invaders of such impoundments in coastal South Carolina.

Algal

Lists of algae associated with wigeongrass in North America are available for British Columbia (Carl 1937), Florida (Gidden 1965), North Carolina (Davis et al. 1985), Saskatchewan (Tones 1976), and Texas (Conover 1964b). *Agardhiella*, *Cladophora*, *Enteromorpha*, *Gracilaria*, *Rhizoclonium*, and *Ulva* are

Table 8. Co-occurrences of wigeongrass (*Ruppia maritima*) in the same water body with

		Reference ^{a,b} (number of species)																																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Species (number of occurrences)		(14)	(12)	(11)	(9)	(9)	(8)	(8)	(7)	(7)	(7)	(7)	(6)	(6)	(6)	(6)	(6)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
<i>Ruppia maritima</i> s.l.	(75)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Potamogeton pectinatus</i>	(41)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x								x	x	x	x		x	x	x	x	x	
<i>Chara</i> spp.	(25)	x	x	x		x	x	x	x		x	x	x	x	x					x	x	x				x	x	x							
<i>Zannichellia</i> spp.	(22)		x	x	x		x	x		x		x		x			x		x						x	x	x					x			
<i>Zostera</i> spp.	(21)			x				x				x		x					x							x					x				
<i>Myriophyllum</i> spp.	(18)	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x											x					x		
<i>Najas</i> spp.	(14)	x		x	x			x	x		x				x		x				x	x							x				x	x	
<i>Halodule wrightii</i>	(12)																						x	x	x										
<i>Potamogeton perfoliatus</i>	(10)					x					x	x	x								x								x		x			x	
<i>Ceratophyllum demersum</i>	(10)	x	x			x	x	x		x				x			x					x				x									
<i>Vallisneria</i> spp.	(6)	x										x				x					x								x				x		
<i>Utricularia</i> spp.	(6)			x			x		x					x			x						x							x					
<i>Ranunculus</i> spp.	(5)			x	x	x		x						x																					
<i>Potamogeton pusillus</i>	(5)				x		x	x																							x				
<i>Thalassia testudinum</i>	(5)																							x	x	x									
<i>Potamogeton filiformis</i>	(5)		x		x			x		x																							x		
<i>Halophila engelmannii</i>	(4)																								x	x	x								
<i>Potamogeton richardsonii</i>	(4)		x	x			x									x																			
<i>Syringodium filiforme</i>	(3)																																		
<i>Ruppia cirrhosa</i>	(2)				x																													x	
<i>Potamogeton bertholdii</i>	(2)												x																						
<i>Ruppia spiralis</i>	(2)																																		
<i>Potamogeton amplifolius</i>	(1)		x																																
<i>Potamogeton crispus</i>	(1)		x																																
<i>Potamogeton praelongus</i>	(1)		x																																
<i>Heteranthera dubia</i>	(1)		x																																
<i>Elodea</i> spp.	(1)		x																																
<i>Potamogeton natans</i>	(1)				x																														
<i>Potamogeton friesii</i>	(1)				x																														
<i>Potamogeton foliosus</i>	(1)				x																														
<i>Hippuris vulgaris</i>	(1)						x																												
<i>Potamogeton vaginatus</i>	(1)							x																											
<i>Callitriche hermaphroditica</i>	(1)										x																								
<i>Ruppia polycarpa</i>	(1)																																		
<i>Ruppia tuberosa</i>	(1)																																		
<i>Lepilaema preissii</i>	(1)																																		
<i>Lepilaema bilocularis</i>	(1)																																		
<i>Lepilaema cylindrocarpa</i>	(1)																																		
<i>Aponogeton</i> sp.	(1)																																		
<i>Cymodocea manatorum</i>	(1)																																		
<i>Potamogeton salvinia</i>	(1)																																		
<i>Posidonia</i> sp.	(1)																																		

^a Reference: 1—Neel et al. 1973; 2—Metcalf 1931; 3—Verhoeven 1980a; 4—Willen 1962; 5—Haag and Noton 1981a; 6—Van Vierssen 1982a; 7—Van Vierssen 1982a; 8—Butler and Hanson 1988 unpubl.; 9—Ravanko 1972; 10—Davis and Carey 1981; 11—Wright et al. 1949; 12—Harris 1952; 13—Kornas et al. 1960; 14—Getsinger et al. 1982; 15—Hammer et al. 1975; 16—Van Vierssen 1982a; 17—Brock and Lane 1983; 18—Klavestad 1957; 19—Vicars 1976; 20—Bolen 1964; 21—Zimmerman and Livingston 1979; 22—Stieglitz 1966; 23—Kochet al. 1974; 24—Van Vierssen 1982a; 25—Van Vierssen 1982a; 26—Kadlec and Smith 1984; 27—Bailey and Titman 1984; 28—Montz 1978; 29—Oberholzer and McAttee 1920; 30—Thorne-Miller et al. 1983; 31—Chamberlain 1960; 32—Riley and McKay 1980; 33—Verhoeven and Van Vierssen 1978b; 34—Anderson 1966; 35—Grontved 1958; 36—Thorhaug et al. 1985; 37—Reynolds and Reynolds 1975; 38—Millard and Scott 1953; 39—Springer and Darsie 1956; 40—Conover 1964b; 41—Gillner 1960 in Chapman 1974; 42—Chapman 1960; 43—Tabb et al. 1962; 44—Orth and Moore 1981; 45—Heitzman 1978; 46—McCarraher 1962; 47—Taylor

other submersed angiosperms and Chara in areas throughout the world.

[illegible]

1939; 48—Strawn 1961; 49—Deevey 1957; 50—Tones 1976; 51—Moyle 1945; 52—Schuler 1987; 53—Correll et al. 1978a; 54—Kemp et al. 1981; 55—Wood 1959; 56—Keddy 1987; 57—Burk 1962; 58—Saunders and Saunders 1981; 59—Robarts 1976; 60—Conover 1961; 61—Florschutz 1959; 62—Hammer and Haseltine 1988; 63—McCarraher 1977; 64—Davis et al. 1985; 65—Nilssen 1975; 66—Eilers 1975; 67—Harrison 1982; 68—Wetzel et al. 1981; 69—Transeau 1913; 70—McMahan 1969; 71—Zieman 1982; 72—Gidden 1965; 73—Pulich 1985; 74—Hellier 1962; 75—Harlin and Thorne-Miller 1981.

^b Duplicated references indicate data from widely separated wetlands.

important wigeongrass associates in thalassic waters of the eastern United States (Springer and Darsie 1956; Conover 1958; Grizzell and Neely 1962; Nixon and Oviatt 1973; Harlin and Thorne-Miller 1981; Thorne-Miller et al. 1983). Several of these genera, as well as *Spirogyra* and *Oedogonium*, are serious reducers of wigeongrass production in coastal salt marsh impoundments managed for wigeongrass (Heitzman 1978). Gilmore et al. (1982) showed how impoundment and flooding of Florida salt marshes replaces emergent vegetation with wigeongrass and various algae. In Europe, *Cladophora*, *Enteromorpha*, and *Vaucheria* are the most common noncharaceous macroalgae associated with wigeongrass (Verhoeven and Van Vierssen 1978b; Van Vierssen 1982a, 1982b). Millard and Scott (1953) noted that *Enteromorpha*, *Cladophora*, *Ectocarpus*, and *Lyngbya* form most luxuriant growths in a South African estuary after the wigeongrass community dies down. *Enteromorpha* is also a common wigeongrass associate in Iraq (Chapman 1960). *Ectocarpus* and *Lamprothamnium* (characeous genera) commonly occur with Australian wigeongrass (Wood 1959; Brock and Lane 1983).

Other algae, including other chlorophytes as well as cyanophytes, rhodophytes, and phaeophytes, coexist with various *Ruppia* taxa (Grontved 1958; Kornas et al. 1960; Ravanko 1972; Hammer et al. 1975; Nilssen 1975; Lindner 1978; Zimmerman and Livingston 1979; Congdon and McComb 1981). Carpelan (1957) and Davis (1978) listed algae associated with wigeongrass in hypersaline solar evaporation ponds.

Algae cause significant reductions in wigeongrass growth by midsummer (Mahaffy 1987; Prevost et al. 1978; Whitman and Cole 1987). Mahaffy (1987) recorded six algal genera that form mats and reduce wigeongrass production in Delaware wetlands. Many algae differ from wigeongrass in dates of peak abundance. Because of their early growth, all European *Ruppia* taxa are able to out-compete benthic macroalgae; however, summer growth of floating macroalgae not only shades out wigeongrass, but weakens stems, increasing susceptibility to damage from wave action (Verhoeven 1980a). Algal mats on the surface of the water column also cause thermal stratification that slows flowering and drupelet production (Richardson 1980). Dense mats of floating filamentous algae that shade out wigeongrass and reduce its biomass and drupelet production are a serious problem for managers of coastal wetlands in the southern and eastern United States (Grizzell and Neely

1962; Joanen 1964; Joanen and Glasgow 1965; Harlin and Thorne-Miller 1981).

Some have suggested that algal mats provide some benefits to wigeongrass. Richardson (1980) noted that mats of filamentous algae that remain moist on the bottom temporarily protect wigeongrass plants and drupelets in areas subject to desiccation. He also observed that algal mats help diminish the effects of wind in roiling sediments and that the shading effect of surface algae limits the growth of both epiphytes and phytoplankton, thereby stimulating wigeongrass growth and fruit production.

In *Ruppia*-dominated systems in Baltic waters, angiosperms and benthic algae account for nearly all of the primary production—contributions by phytoplankton are minor (Ankar and Elmgren 1977). Similarly, Gallup (1978) noted that phytoplankton productivity was relatively low in a saline Alberta wetland where wigeongrass was the dominant macrophyte and productivity of benthic algae was extremely high.

Nevertheless, in some situations phytoplankton can greatly lower wigeongrass production and limit distribution of the plant to very shallow (<40 cm) waters (Verhoeven 1980a). Alternating dominance by wigeongrass and phytoplankton was recorded by Flores-Verdugo et al. (1988) in a shallow, river-fed Mexican lagoon having an ephemeral outlet to the ocean. They hypothesized that the cycle is controlled by the occurrence of rainfall and subsequent river flow that brings nutrients into the lagoon, opens the inlet to the ocean, and flushes out existing wigeongrass beds. They also believed that nutrients promote light-limiting blooms of phytoplankton, but when river flows cease, phytoplankton growth diminishes, and wigeongrass exploits nutrients to grow in sediments not readily available to the phytoplankton. Nevertheless, there is poor understanding of the cycles between dominance by phytoplankton, macroalgae, and submersed angiosperms in wetlands (Gibbs 1973).

Because wigeongrass frequently assimilates essential gases and nutrients from the water column, epiphytes can seriously reduce wigeongrass biomass and propagule formation by inhibiting nutrient uptake and photosynthesis (Conover and Gough 1966; Richardson 1980). Peak epiphyte populations coincided with rapid decay of wigeongrass in a Massachusetts estuary (Conover 1958). In a Maryland river, Anderson (1966) and Anderson et al. (1968) found fall densities of the epiphytic diatom *Melosira arenaria* great enough to visually obscure the presence of

wigeongrass; *Cladophora* and *Merismopedia* (a blue green) are also epiphytic there. Blades of wigeongrass in a North Carolina estuary develop a rich epiphytic and animal biota during the growing season (Copeland et al. 1974). In a South African estuary, *Ectocarpus* sp., *Polysiphonia* sp., *Rhodochorton* sp., *Cladophora* sp., and *Rhizoclonium* sp. heavily coat wigeongrass (Scott et al. 1952). Sullivan (1977) listed 57 epiphytic diatom taxa found on wigeongrass in thalassic New Jersey wetlands. These algae formed a golden brown felt completely covering the leaves; *Navicula pavillardii* was the most abundant taxon. However, in other thalassic habitats (Grontved 1958; Wood 1959; Kornas et al. 1960; Zimmerman and Livingston 1979; Congdon and McComb 1981) and in rivers (Conover and Gough 1966; Richardson 1980), wigeongrass is relatively free of epiphytes, perhaps because of grazing invertebrates or current flow.

The only instance I found where epiphytes were said to possibly benefit wigeongrass was the account by Flores-Verdugo et al. (1988), reporting that a second, smaller crop of wigeongrass had a heavy cover of epiphytes but may have benefited somewhat by their nitrogen-fixing properties. Howard-Williams and Allanson (1981) suggested that epiphytic growth helps another submersed angiosperm (*P. pectinatus*) absorb P.

Diseases and Parasites

Wigeongrass probably is less troubled with diseases than several other submerged angiosperms. Hisinger (1887) stated that "tubercles" on *Ruppia* are a pathological response to the fungus *Tetramyxa parasitica*. Vegetative reproduction usually allows wigeongrass to survive *Rhizoctonia* infestations (Bourn and Jenkins 1928). Motta (1978) collected 24 fungal isolates from Chesapeake Bay wigeongrass; although he determined no specific host-parasite relations, the evidence suggested that some pathogenic activity existed.

Invertebrate

Wigeongrass provides cover for many estuarine and marine invertebrates (Bourn and Cottam 1939; Day 1952; Kerwin et al. 1975 in Stevenson and Confer 1978), and wigeongrass detritus is an important food source for invertebrates (Tenore 1972; Nixon and Oviatt 1973; Edwards 1978; Verhoeven 1978). Lists

of invertebrates found with wigeongrass or in impoundments managed for the plant are available for Africa (Scott et al. 1952; Millard and Scott 1953), Australia (Geddes et al. 1981), California (Carpelan 1957), France (Hoffman 1958), Maine (Hyer 1963), Mexico (Edwards 1978), North Carolina (Heitzman 1978), Saskatchewan (Hammer et al. 1975; Tones 1976), South Carolina (Taniguchi 1986; Wenner and Beatty 1988), Sweden (Ankar and Elmgren 1977), and Texas (Hellier 1962; Johnson 1974).

Invertebrates associated with *Ruppia*-dominated communities in western Europe number up to 43,800/m² with biomasses of up to 22.9 g/m² ash-free dry weight (Verhoeven 1980a). Verhoeven (1980a) found that only 15 of 75 species intimately associate with wigeongrass plants, that only one or two species strongly dominate, and that poor correlations exist between numbers of species and plant biomass or water salinity. Van Vierssen (1982a) listed many invertebrates found in European waters inhabited by wigeongrass and noted that faunal diversity decreases from north to south as salinity fluctuations increase. Hoffman (1958) also found relatively low invertebrate diversity in European wigeongrass communities.

Many mollusks, polychaete worms, crustaceans, and an echinoderm inhabit a Florida bay dominated by *Halodule wrightii* and lesser amounts of wigeongrass when salinities are 18–35 g/L; the echinoderm disappears when salinities fall to 5–18 g/L, and *Chara* becomes codominant with wigeongrass (Tabb et al. 1962). Carl (1937) listed invertebrates of a wigeongrass-dominated lagoon in British Columbia where salinity varies from nearly 0 g/L in winter to 17.7 g/L in summer. Rotifers, polychaetes, nematodes, gammarid amphipods, and grass shrimp (*Paleomonetes* spp.) associate with wigeongrass in a North Carolina estuary where salinity is usually 3–10 g/L (Copeland et al. 1974).

As wigeongrass beds are fragmented by wave action from fall winds, the floating masses are eaten and turned into smaller particles by gammarids and isopods; this stimulates a large detrital food chain (Verhoeven and Van Vierssen 1978b). In a New England bay, Nixon and Oviatt (1973) found that amphipods are abundant in wigeongrass detritus. The soft, highly organic sediments where the plants grow were suitable for small worms, nematodes, ciliates, ostracods, and copepods; however, these substrates were poor for large infaunal invertebrates. Poff (1973) reported that the annelid worm *Pelosclex gabriellae* disappears when wigeongrass does in a Texas

bay. Heck and Orth (1980) listed temporal and diel variation in use of mixed *Ruppia*-*Zostera* meadows by decapod crustaceans in the Chesapeake Bay. Conover (1961) found abundant zooplankton in Rhode Island waters that supported better stands of wigeongrass. Jones (1975) correlated a decrease in macrozooplankton with a decline in wigeongrass in a Texas bay and noted that some invertebrates use the plant as an attachment site for eggs.

Invertebrates can benefit wigeongrass. Grazing on wigeongrass epiphytes by snails (Richardson 1980) and amphipods (Greze 1968; Zimmerman et al. 1979; Van Montfrans et al. 1984) increases fruit production.

I found little information on the direct consumption of living wigeongrass by invertebrates. Edwards (1978) noted that wigeongrass is the main food of the gastropod *Cerithidea mazatlanica* in a Mexican lagoon. Among the seven most common invertebrates in a Netherlands pond, only *Gammarus zaddachi* directly consumes *Ruppia cirrhosa* (Verhoeven 1978). Nevertheless, the animal may reduce fall biomass of this plant by nearly 40%. Copeland et al. (1974) showed wigeongrass as a major food item of marine crabs (*Callinectes* spp.) in a North Carolina estuary. Zieman (1982) reported that the blue crab (*Callinectes sapidus*) consumes *Ruppia* in south Florida.

Data on concentrations of various insecticides found in irrigation drainwater evaporation ponds supporting wigeongrass is available (Schroeder et al. 1988).

Amphibian and Reptile

In an African estuary, Millard and Scott (1953) found *Rana* and *Xenopus* tadpoles common where wigeongrass was abundant. Water snakes (*Nerodia sipedon*) and American alligators (*Alligator mississippiensis*) are regularly observed in wigeongrass impoundments in the southeastern United States (Heitzman 1978; Epstein and Joyner 1986). The plant can be an important food of some sea turtles (Felger et al. 1979).

Fish

Fish extensively use wetlands dominated by wigeongrass (Carl 1940; Chapman 1960; Scott et al. 1952; Millard and Scott 1953; Hellier 1962; Jeffries 1972; Nixon and Oviatt 1973; Edwards 1978).

Verhoeven and Van Vierssen (1978b) and Verhoeven (1980a) found fish in all except the smallest *Ruppia*-dominated habitats in western Europe. Copeland et al. (1974) listed permanent resident, seasonal (absent in winter), and migrant fish in a wigeongrass-dominated North Carolina estuary, and Heitzman (1978) listed the fresh- and saltwater fish that live in impoundments in that state, many of which are managed for wigeongrass. Species compositions of fish in South Carolina wigeongrass impoundments and adjacent tidal wetlands are compared by Wenner et al. (1986). A few fish species eat wigeongrass and its detritus but probably more often use stands as a nursery (Hildebrand and Cable 1938; Sculthorpe 1967; Austin and Austin 1971; Congdon and McComb 1981).

Of the many fish species that use wigeongrass beds in the lower Chesapeake Bay, only one group, consisting of two combtooth blennys (*Hypsoblennius hentzi* and *Chasmodes bosquianus*), a toadfish (*Opsanus tau*), and a sea bass (*Centropristis striata*), likely prefer these beds to adjacent beds of *Zostera* (Weinstein and Brooks 1983). Of 22 fish species that use the wigeongrass-dominated saline lagoons of the Camargue, France, seven—including the common carp—are of freshwater origin (Hoffman 1958). Greatest fish use of *Ruppia*-dominated coastal wetlands occurs in spring and fall (Nixon and Oviatt 1973). In a Florida bay, Tabb et al. (1962) found more fish, but less wigeongrass, at salinities of 18–35 g/L than at 5–18 g/L. Davis (1978) listed marine fish occurring in hypersaline (50–73 g/L) solar evaporators dominated by wigeongrass. Changes in fish populations occurred, along with increases in wigeongrass, when an additional ship canal was opened from the lower Laguna Madre, Texas, to the Gulf of Mexico (Breuer 1962).

Wigeongrass can also provide excellent food and cover for fish in some inland waters (Terrell 1923). Certain saline (about 19–31 g/L) lakes contain wigeongrass and fish (e.g., *Cyprinodon*, *Coregonus*, *Pungitius*), but most saline interior wetlands are generally inhospitable to fish (Navarre 1959 in Cole 1963; Hammer et al. 1975; Tones 1976).

Fish seldom consume large amounts of wigeongrass. Carr and Adams (1973) found low consumption of wigeongrass among 10 dietary groups of Florida fish; of 21 species, only three had a herbivorous stage. In Louisiana, only the gulf sheepshead (*Archosargus oviceps*) eats significant amounts (Darnell 1958). Nevertheless, when usual sources of essential fatty acids for fish and invertebrates are exhausted

in tidal marshes, wigeongrass sometimes provides these nutrients (Jeffries 1972).

Fish can negatively affect their association with wigeongrass by raising turbidity and thus limiting wigeongrass growth in wetlands having easily resuspendible bottom sediments; young plants are especially vulnerable to such light limitation (Joanen 1964; Joanen and Glasgow 1965). Conversely, some fish feeding likely aids the dispersal of wigeongrass drupelets, and the germination rate of drupelets passing through the digestive systems of some fish can greatly increase (Agami and Waisel 1988). Grizzell and Neely (1962) believed that fish consumption of algal scums benefits wigeongrass.

Bird

Many water birds eat wigeongrass vegetation and drupelets. The invertebrates that birds find in living and decomposing wigeongrass are also important foods (Nixon and Oviatt 1973; Verhoeven and Van Vierssen 1978b). Unfortunately, agricultural land development and the construction of irrigation reservoirs have destroyed or seriously degraded many of the vast natural beds of wigeongrass in coastal and interior Mexico (Saunders and Saunders 1981). These beds helped support huge numbers of wintering water birds from all over North America.

In subtropical climates, wintering waterfowl quickly consume entire stands of wigeongrass (Heit 1948) but, with proper water-level manipulations in managed impoundments, stands reestablish in only a few weeks (Jemison and Chabreck 1962; Joanen 1964; Joanen and Glasgow 1965). Stieglitz (1966) believed that waterfowl can consume at least 50% of the standing crop without damaging stands. Australian black swans (*Cygnus atratus*) can eat 20% of the standing crop (Congdon and McComb 1981). A major problem for managers of coastal impoundments in the southeastern United States is high summer temperatures—these can prevent the fall growth of wigeongrass on which wintering waterfowl largely depend (Kelley and Porcher 1986).

Hurricanes along the gulf coast may spread wigeongrass into nearby interior wetlands where it then receives increased use by waterfowl (Kimble and Ensminger 1959). Similarly, cyclic changes in the vegetation of climatically unstable prairie wetlands cause changes in species composition of waterfowl that eat the vegetation or its associated invertebrate fauna (Swanson et al. 1988). Cycles of

dominance by *Potamogeton pectinatus* and *Ruppia maritima* are fairly common in saline wetlands in this region as dissolved salts are alternately diluted and concentrated (H. A. Kantrud, personal observation).

Studies throughout the world confirm the attractiveness of wigeongrass or *Ruppia*-dominated wetlands to waterfowl and show that all parts of the plant are eaten. Swiderek (1982) showed that some waterfowl species feed mainly on wigeongrass drupelets, whereas others select the vegetative portions of the plants. Over 5,000 wigeongrass drupelets can be found in one duck (McAtee 1915; Kubichek 1933). Table 9 suggests that wigeongrass is primarily a food of dabbling ducks (Anatini) and pochards or diving ducks (Aythyini). The plant also rates as good food for geese (Anserini; McAtee 1939; Quay and Critcher 1962) and swans (Cygnini; McAtee 1939; Sincock 1962; Gaevskaya 1966; Congdon and McComb 1979, 1980, 1981). Saunders and Saunders (1981) reported use by whistling-ducks (Dendrocygnini).

Certain ducks seem especially fond of wigeongrass. In South Carolina, Gordon et al. (1987) and Gray et al. (1987) reported that communities where *Ruppia maritima* and *Eleocharis parvula* codominate are intensively used by wintering green-winged teals (*Anas crecca*), northern pintails (*A. acuta*), and American wigeons (*A. americana*). A coastal Massachusetts impoundment supporting wigeongrass was especially attractive to American black ducks (*A. rubripes*; Portnoy et al. 1987). Euliss (1989) noted that, in irrigation wastewater evaporation ponds in California, American wigeons and redheads (*Aythya americana*) eat and uproot wigeongrass vegetation in deeper open water areas; northern pintails then feed mostly on drupelets from the plants that wash ashore. Wigeongrass-dominated wetlands in North Dakota were especially attractive to fall migrant gadwalls (*Anas strepera*), American wigeons, and redheads (H. A. Kantrud, personal observation).

Intensive feeding on wigeongrass by swans may significantly disturb anaerobic bottom sediments and affect turnover rates of organic materials and increase nutrient release (Congdon and McComb 1980).

Wigeongrass is often a food of coots (*Fulica* spp.; Quay and Critcher 1962; Gaevskaya 1966; Holmes 1972; Prevost et al. 1978; Verhoeven and Van Vierssen 1978b; Swiderek 1982) and other aquatic birds (Sculthorpe 1967). Verhoeven (1978) calculated the consumption of *Ruppia cirrhosa* by individual coots as 70 g/day dry weight and estimated that about

Table 9. *Use of wigeongrass (Ruppia maritima) as food by groups of waterfowl.*

Reference	Waterfowl (general)	Dabbling ducks	Diving, sea, and stiff- tailed ducks	Geese and brant	Swans
Nuttall 1834			1		
McAtee 1915		3,4,5	3		
McAtee 1918		1			
Mabbott 1920		3			
Oberholzer and McAtee 1920	1				
Wetmore 1921	3,4,5				
McAtee 1922		1			
Phillips 1923	1				
Terrell 1923	1				
Metcalf 1931	1				
Bourn 1932	1				
Kubichek 1933			3		
Cottam 1934	1				
McAtee 1935	2				
Martin and Uhler 1939	3,4,5				
McAtee 1939		2	2	2	2
Steenis 1939	1				
Cottam et al. 1944				1	
Addy 1946		1			
Campbell 1946		3,4,5			
Heit 1948	1				
Critcher 1949	1				
Wright et al. 1949	1				
Yancey 1949			1		
Singleton 1951	1				
Smith 1951		3,4,5			
Yocom 1951			1		
Harris 1952	1				
Hancock 1953	1				
Spencer 1953	1				
Rawls 1954			1		
Scott 1954	1				
Beter 1957		1			
Gates 1957		1			
Hoffman 1958		1			
Kimble 1958		1	1		
Neely 1958	1				
Stewart and Manning 1958					2
Chamberlain 1959		3		3	
Davison and Neely 1959	1				
Chamberlain 1960	1				
Jemison 1961	1				
Yocom and Keller 1961		1	1		
Grizzell and Neely 1962	1				
Jemison and Chabreck 1962	1				
Neely 1962	1				
Quay and Critcher 1962	1			1	
Sincock 1962	1		1		1
Stewart 1962		3,4	3,4	3,4	1

Table 9. *Continued.*

Reference	Waterfowl (general)	Dabbling ducks	Diving, sea, and stiff- tailed ducks	Geese and brant	Swans
Hartman 1963		1			
Joanen 1964	2				
Gore 1965	1				
Joanen and Glasgow 1965	2				
Savage 1965			3		
Gaevskaya 1966				1	1
Neely and Davison 1966	1				
Rogers and Korschgen 1966			1		
Stieglitz 1966	1				
Cronan and Halla 1968		1	1		
McMahan 1970		1	1		
Tamisier 1971		3			
Erskine 1972			1		
Holmes 1972		1			
Kerwin and Webb 1972		4,5			
Stieglitz 1972		1			
Nixon and Oviatt 1973		1			
Johnsgard 1975		3,4			
Penkala 1975				1	
Bellrose 1976		4			
Landers et al. 1976		1	1		
Morgan et al. 1976		1	1		
Serie and Swanson 1976		4			
Krapu and Swanson 1978		3			
Prevost et al. 1978		3			
Verhoeven and van Vierssen 1978b		1	1		1
Congdon and McComb 1979					1
Verhoeven 1979		1	1		1
Congdon and McComb 1980					1
Congdon and McComb 1981	1				1
Saunders and Saunders 1981		3,4	3	1	
Paulus 1982		1			
Swiderek 1982		3,4,5	3		
Bailey and Titman 1984			4,5		
Mahaffy 1987	2				
Schuler 1987		1			
Strange 1987		1			
Euliss 1989		3	1		

^a1 = No specific plant parts mentioned; 2 = whole plant; 3 = drupelets; 4 = leaves, "foliage" or "vegetation"; 5 = rhizomes or stems.

20% of the fall decrease in biomass of this plant is from bird grazing. Waterfowl and coots exploit the *Ruppia* beds of western Europe mostly from the end of summer to winter (Verhoeven and Van Vierssen 1978b) and the birds help disperse drupelets (Verhoeven 1979).

Wigeongrass is sometimes an important food of red knots (*Calidris canutus*); dowitchers (*Limnodromus* spp.) and common snipes (*Gallinago gallinago*) also eat the plant (Sperry 1940). Martin et al. (1951) also reported use of wigeongrass by knots and dowitchers, as well as by other *Calidris* spp., and by purple

gallinules (*Porphyryla martinica*), black-necked stilts (*Himantopus mexicanus*), and king rails (*Rallus elegans*). Bourn and Cottam (1950) indicated that wigeongrass was a minor food of various rails (*Rallus* spp.), yellowlegs (*Tringa* spp.), and willets (*Catoptrophorus semipalmatus*). Allen (1956) considered wigeongrass an important food of flamingos (*Phoenicopterus* spp.).

The animal community associated with wigeongrass is an important food source for many breeding and wintering birds (Hoffman 1958; Verhoeven and Van Vierssen 1978b). A bewildering array of wintering and migrating wading birds, shorebirds, and waterfowl use South African estuaries ("vleis") where *R. maritima* and *Zannichellia aschersoniana* are often dominant and large numbers of invertebrates occur (Millard and Scott 1953; Scott 1954). A wide variety of birds also use *Ruppia*-dominated impoundments in the southeastern United States (Epstein and Joyner 1986). In these areas, the plant beds probably also provide foods for insect-hawking birds such as swifts (Apodidae), swallows (Hirundinidae), and martins (Hirundinidae). Morgan (1954) commented on the large numbers of invertebrate waterfowl foods found in an Australian wetland dominated by wigeongrass and *Potamogeton pectinatus*.

Mammal

The only wild mammals known to consume living wigeongrass are West Indian manatees (*Trichechus manatus latirostris*; Hartman 1971), muskrats (*Ondatra zibethicus*; McCabe 1982), and nutria (*Myocastor coypus*; R. H. Chabreck, personal communication in Garner 1962). Deer and cattle sometimes eagerly eat detached plants windrowed along shorelines (Campbell 1946).

Economics

I have not tried to estimate the economic value of wigeongrass, but the figure must be great when one considers that wigeongrass-dominated communities receive extensive use by aquatic animals important to commerce and sport. Warne (1971 in Eilers 1975) found that wigeongrass stands in coastal lagoons dampen incoming waves and collect sediment and floating debris. A small additional economic value can be inferred from Davis (1978), who

noted that wigeongrass and its associated algal community traps silt and helps seal the bottoms of solar evaporators, thus making the salt recovery operation slightly more efficient.

Wigeongrass apparently is not a great economic problem. The plant does not seriously clog irrigation or mosquito control ditches or greatly degrade fishponds or swimming areas as do many other submersed macrophytes. Plants sometimes hinder boat traffic (Carl 1937; McMahan 1969), however, or are a temporary nuisance at beaches when washed ashore in large quantities (Conover 1958; Haag and Noton 1981b).

Propagation and Management

Since the early 1930's, impounded wetlands, where wigeongrass and other hydrophytes are grown for waterfowl food, have been reclaimed from colonial-age rice paddies along the coast of the southern and southeastern United States (Tiner 1977; Davis et al. 1985). In this locality, individual management units can contain over 4,000 ha of such impoundments (Sandifer et al. 1980). Many former ricefields in this area, some in existence since the mid-1700's, were converted to hunting preserves around the turn of this century and are now similarly managed (Miglares and Sandifer 1982). Problems with wigeongrass management in these wetlands include low vegetative and drupelet production, high turbidity, shading by filamentous algae, invasion by fish and introduced plants, silt and detritus accumulations, and acidification of bottom sediments caused by the oxidation of iron polysulfides. Initial research findings and suggestions on how to manage these wetlands for good wigeongrass production appeared in the fifties and sixties (Neely 1958, 1962; Davison and Neely 1959; Grizzell and Neely 1962; Jemison and Chabreck 1962; Joanen 1964; Joanen and Glasgow 1965; Baldwin 1968). A summary of this information advises that, to help produce good stands, these factors are necessary: (1) periods of stable water levels during the growing season, (2) water depths of 0.15–0.76 m, (3) water salinities of 4.9–11.5 g/L, (4) pH 7.0–8.0, (5) substrate salinities <1.12%, and (6) turbidities <35 ppm. Complete summer drawdowns with fall reflooding help keep bottoms firm and eliminate most undesirable fish. However, young mullet (*Mugilidae*) given access to these wetlands may help control shading from filamentous algae. Partial drawdowns in early spring or fall also stimulate wigeongrass production. Removal of stained or acidic

fresh water helps maintain proper pH and gives some protection to native emergent plant communities at the edges of impoundments. Periodic flushing with fresh water aids drupelet germination and also helps prevent algal buildups.

Techniques to encourage wigeongrass growth in these impoundments were refined during the seventies and eighties. Wilkinson (1970) noted steadily increasing frequency of wigeongrass for 3 years in a newly constructed South Carolina impoundment, where brackish water was held at 0.61 m except during February, when it was drained. Morgan (1974) and Morgan et al. (1976) recommended raising water levels slowly during the growing season or taking in seawater during spring tides; draining ponds every 2 years; and keeping salinities around 8.75 to 17.5 g/L to discourage possible macrophyte competitors. Heitzman (1978) noted that, after several years of stable water levels, silt and detritus accumulations deeper than about 4 cm will not provide a good rooting medium for wigeongrass and expose stands to rapid elimination by wave action. At that time, it is necessary to temporarily drain impoundments to a moist-soil condition to compact and oxidize bottom substrates and restore productivity.

For ponds in the 5.0–20.0 g/L salinity range, Prevost (1987) recommended (1) lessening acidity by lowering water during March to May (for 2–8 weeks) to levels that keep the bottom saturated but free of surface water; (2) stabilizing soils and reducing turbidity by lowering water levels for 1–2 weeks in late spring or early summer to 25–46 cm below the bottom surface; (3) reflooding ponds to 15–20 cm; and (4) controlling algae by gradually raising water levels to 46–76 cm in summer and early fall while maintaining water circulation. For ponds with salinity in the 20.0–30.0 g/L range, he recommended similar techniques—but for ponds in this range that are dry for several years, he suggested trying to raise bottom substrate pH by changing water 2–3 times at 4–6 week intervals during the growing season. For ponds with >30.0 g/L salinity, management involves tidal flooding in early spring and diluting with fresh water later in the growing season.

Recent observations on wigeongrass in coastal California impoundments have indicated that acidity in heavy clay soils can best be reduced by very slow reflooding rather than a regime of rapid reflooding and flushing (B. Smith, California Department of Fish and Game, personal communication). Additional details are available on construction, management, and maintenance of coastal wigeongrass impoundments (Epstein et al. 1986;

South Carolina Sea Grant Consortium 1987).

A different situation for wigeongrass management exists in the wetlands of the Great Basin, where soil salinities are often too high to support the plant. Here, *Salicornia*-dominated salt flats lying near sources of freshwater inflow are diked and flooded with 45–60 cm of fresh water. After an initial growth of *Chara*, impoundment water levels are maintained at about 35 cm to maintain wigeongrass and other submersed macrophytes that prosper under reduced soil salinities (Kadlec and Smith 1989).

At least in the southeastern United States, an added benefit of dewatering wigeongrass ponds to substrate levels is the growth of clumps of emergent hydrophytes that later reduce the destructive effects of wave action (Swiderek 1982). Heitzman (1978) noted that failure to harvest muskrats can result in total loss of such emergents but that far more damage to submersed macrophytes can occur when burrowing causes dike damage that drains impoundments.

Techniques to harvest and plant wigeongrass have been known for many years. To obtain drupelets, McAtee (1915) suggested gathering them from the upper part of plants to reduce unwanted material and allow for better air circulation. He also recommended wet cold storage if drupelets are not planted immediately and soaking them thoroughly before planting so they will sink. Terrell (1923) recommended planting five bushels per acre (4.4 hL/ha), either rhizomes or whole plants, in brackish or saline water 0.3–1.5 m deep. Joanen and Glasgow (1965) stated that the general techniques of Martin and Uhler (1939) for harvest, storage, and planting of submersed hydrophytes will work for wigeongrass. Stands can be established by imbedding drupelets or leafy stems in clay balls and dropping them overboard (Steenis 1939) or by merely scattering plants on the water, preferably in spring (Neely 1962). Donnelly (1968) successfully planted wigeongrass with 15-cm² plugs of bottom substrate, presumably containing rhizomes, roots, drupelets, and portions of stems.

Gore (1965) noted good spring germination of fall-collected drupelets stored in brackish water in a refrigerator at 0.5° C. Recent work by Seeliger et al. (1984) and Koch and Seeliger (1988) suggested that better germination of wigeongrass drupelets results when storage conditions are geared to the general environmental conditions of the wetland where the drupelets are collected and the life-cycle characteristics of the plants in that wetland.

Information on artificial or induced establishment of submersed hydrophytes was reviewed by Kadlec

and Wentz (1974). They provided lists of plant suppliers, techniques for propagule harvest, storage, and planting, and methods for site preparation.

The impoundment of coastal wetlands to produce wigeongrass and other plants has created favorable habitat for many other organisms besides wintering waterfowl. Nevertheless, the desirability of impounding more tidal wetlands has come under increased scrutiny in some States because these habitats are unsuitable for certain economically important marine fish and other organisms (Gilmore 1987). Overall, however, it is likely that water pollution, dredging, and changes in water regimes caused by dam operations have been far more damaging to marine biota than have these waterfowl impoundments.

Control Methods

Wigeongrass is a relatively innocuous plant compared to other submersed or floating hydrophytes that are notorious nuisances to man—*Myriophyllum spicatum*, *Hydrilla verticillata*, and *Alternanthera philoxeroides*, to name a few. Most information on control of wigeongrass has been incidentally gained during efforts to eradicate other species. Some of the chemicals mentioned in the next paragraph may be considered unsafe for application to aquatic environments, and no endorsement of the use of any particular chemical is implied or intended. Readers are advised to strictly adhere to application instructions on pesticide labels formulated by the Environmental Protection Agency.

Sodium arsenite was once listed for controlling wigeongrass (Davison et al. 1962), but the many dangers involved with the use of this chemical soon rendered it obsolete. Stevenson and Confer (1978) reported control with atrazine at 1.0 ppm and postulated that similar control is achieved with 0.25–0.50 ppm. Wigeongrass greatly decreased within 6 weeks after receiving 2,4-D ester at 112 kg/ha, and only small numbers of plants were present 4 years after application (Getsinger et al. 1982). Correll et al. (1978a, 1978b) suggested that alachlor and atrazine in runoff from agricultural fields lowers biomasses of wigeongrass and other submersed macrophytes in Chesapeake Bay. Concentrations of a large variety of herbicides in irrigation drainwater ponds supporting wigeongrass are listed in Schroeder et al. (1988).

References on biological control of wigeongrass are few. Aquarium tests of Duthu and Kilgen (1975) showed that white amur—common carp hybrids

(*Ctenopharyngodon idella* × *Cyprinus carpio*) ate moderate amounts of wigeongrass. Buckingham (1982) raised at least one generation of the aquatic moth *Parapoynx diminutalis* on wigeongrass in quarantined indoor tests. This insect was being tested for control of nuisance hydrophytes. A recent literature search by Elakovich and Wooten (1987) showed that no known allelopathic plants affect wigeongrass and that wigeongrass produces no allelopathic effects on other plants.

Research Needs

The many factors affecting submersed macrophytes involve dozens of scientific fields. An outline of the research needs within these many disciplines is beyond the scope of this review. Therefore, I will mostly discuss problems of immediate concern to wetland managers and waterfowl biologists and give only a few examples of basic research needs.

Of the hundreds of species of submersed macrophytes, only a few, such as wigeongrass, *Potamogeton pectinatus*, and *Zostera* spp., are of nearly worldwide importance as foods of waterfowl and other aquatic wildlife. Traditional access to these few foods probably determines the routes, migration chronologies, and wintering areas for many species of waterfowl. Thus, the priority of conservationists should be to determine the historic range of wigeongrass and then conduct systematic surveys to inventory existing natural stands so that plans to restore and protect their populations can be formulated.

Perhaps the greatest challenge for waterfowl managers is to find economical methods to restore populations of wigeongrass and other desirable waterfowl food plants to natural and impounded wetlands, where conditions have become so unsuitable that these plants have mostly disappeared or no longer can survive. Death of the submersed macrophyte community can also drastically deplete populations of macroinvertebrates that are also choice waterfowl foods (Davies 1982).

Problems of low wigeongrass production usually are related to excessive turbidity. Butler and Hanson (1990, unpublished data) showed that the causes of turbidity vary seasonally and are often difficult to determine. In the relatively large, eutrophic prairie lake they studied, turbidity was related to resuspension of fine particulates from wave action, precipitation of calcite in the water column, growths of planktonic algae, and, to a much lesser extent, resuspension of sediments by rough fish. They found that the removal of planktivorous fish resulted in

greatly increased populations of filter-feeding zooplankton that fed heavily on planktonic algae. Within 1 year, great increases in water clarity resulted, not only from the decreases in algae, but from the removal of detrital and inorganic particulates. Wigeongrass and other submersed angiosperms grew vigorously in response to the much improved light climate. By the second and third years, luxurious beds of these plants were effective in further increasing water clarity, either through protecting sediments from resuspension, limiting phytoplankton populations by competition for light or other resources, or producing compounds toxic to algae. Further research and monitoring of this lake will be required as it responds to these physical and biological changes. Similar biomanipulation experiments are needed to discover methods to ameliorate light-limiting turbidity; to understand trophic interactions between benthic omnivorous fish, planktivorous fish, zooplankton, and phytoplankton; and to determine their effects on water chemistry and vascular plant communities. As suggested by Spencer and King (1984), can manipulation of fish populations through stocking or removal—or indirectly through altering their prey or habitat—economically increase wigeongrass and other valuable waterfowl food plants in a variety of wetland types?

Managers are often asked that impoundments be managed simultaneously for irrigation, flood control, recreational boating, sport fishing, and waterfowl hunting. Undue water-level fluctuations and water shortages are common features of many of these wetlands. Therefore, it is especially important that managers be able to predict the effects of water level manipulations on submersed macrophytes at various times of the year and across a wide range of environmental settings.

In coastal areas, impoundments are common wherein water regimes can be controlled for the single purpose of establishing and maintaining wigeongrass and other valuable waterfowl foods; fairly sophisticated techniques have been developed to manage these wetlands. But in other regions, research will be required to develop techniques to control turbidity, excessive emergent vegetation, undesirable fish, and siltation in such impoundments. Cooke (1980) called for research to determine proper dewatering intervals, effects the season of dewatering has on such intervals, and effects of dewatering on sediment and water-column chemistry. He also suggested enhancing the efficacy of dewatering techniques by combining them with other plant management methods. Finally, he emphasized

the need to develop better methods of evaluating techniques used to manipulate vegetation. This approach should lead to the development of standardized methods applicable to different regions or wetland types and would allow managers to compare results.

To determine factors that lower productivity and species diversity, we need controlled experiments to simulate the effects of human developments on a range of wetland types. In heavily populated areas, common problems of eutrophication, disturbance, and siltation are often complicated by the effects of special industrial effluents, thermal pollution from electrical power plants, and hydrological changes resulting from dredging and filling operations. Other areas are affected by oil spills, irrigation wastewater, and increased use of complex agricultural chemicals. We need major advances in pollution and soil erosion control technology to solve these problems.

Research should intensify studies of genetic adaptations of wigeongrass because it is disposed to survival with changes in environmental factors. Van Wijk (1988, 1989) and Van Wijk et al. (1988) describe genetic adaptations to salinity and other habitat factors that determine whether a submersed macrophyte reproduces sexually or asexually. Through reciprocal transplant experiments, the studies could include factors such as substrate type, nutrient availability, or water level fluctuation. The information could identify *Ruppia* genotypes that could be used to revegetate seriously altered or disturbed aquatic ecosystems.

Finally, it must be emphasized that our ability to manage wetlands for wigeongrass production or predict the fate of standing crops cannot be fully realized until we understand the basic patterns of energy flow, resource partitioning, and community dynamics in littoral ecosystems. For example, our poor understanding of factors influencing algal and macrophyte productivity greatly limits our ability to address basic questions, such as whether herbivory or detritivory fuel secondary production in these ecosystems (Murkin 1989). Similarly, much research is needed to determine whether herbivory on standing stocks of submersed plants by organisms other than waterfowl is an important factor in regulating their seasonal abundance (Sheldon 1987). Competition between *Ruppia* and *Potamogeton pectinatus* has been stated to occur in certain brackish waters (Howard-Williams and Liptrot 1980), but the basic question of whether competition is important in determining the distribution of submersed plants in general remains unanswered (Rorslett 1987).

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